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# **Genetic and non-genetic evaluation tools for accelerating improvement in beef cattle carcass traits within and across country**



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In the college of

Medicine and Veterinary Medicine,

University of Edinburgh

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**Declaration**

I declare that this thesis is my own composition and that the research described in it is my own work, except where acknowledged. The work described has not been submitted for any other degree or professional qualification.

Tanya Englishby

27<sup>th</sup> September 2017

## **Publications**

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**Abstract**

The main revenue source for beef cattle farmers is the price they are awarded for carcasses based on carcass value (i.e., carcass weight, conformation and fat score) which is influenced by genetic and environmental factors (e.g., herd management). In order to improve profitability, accurate means of evaluating and improving both sets of factors influencing carcass trait performance are necessary. This would entail optimal management of genetic resources and herd practices. Furthermore, access to a large international germplasm pool would facilitate faster genetic gain.

The objective of this thesis was to generate tools for the enhancement of carcass trait genetic and herd management evaluations both at a national and international level. The data used in the thesis originated from the Irish and UK national cattle databases and consisted of 336,944 Irish and 147,876 UK cattle of multiple beef and dairy breeds from 9,572 Irish and 3,385 UK commercial herds.

Livestock mature at different rates depending on a number of factors including the genetic background; therefore, the optimum age at which to slaughter the progeny of different sires may differ. Chapter 2 examined sire level genetic profiles for three carcass traits (carcass weight, conformation and fat score) in cattle using data from the Republic of Ireland. Variance components for each trait across age at slaughter were estimated using sire random regression models. Heritability estimates of carcass traits across ages at slaughter varied depending on gender (heifers, steers, young bulls) and the trait in question, and ranged from 0.08 ( $\pm 0.02$ ) to 0.34 ( $\pm 0.02$ ) for carcass weight, from 0.24 ( $\pm 0.02$ ) to 0.42 ( $\pm 0.02$ ) for conformation score and from 0.16 ( $\pm 0.03$ ) to 0.40 ( $\pm 0.02$ ) for fat score. Genetic correlations between traits across ages at slaughter were all significantly less than unity, indicating that different genetic

mechanisms control these traits across life. The results from chapter 2 show that genetic variability in the progeny growth trajectory of sires exists and that this variability in the growth profiles of sires for carcass traits may be exploited in breeding programmes.

As carcass traits are a function of both the genetics of the animal and the environment in which the animal is reared, chapter 3 aimed to quantify the contribution of the herd environment to the same three beef carcass traits, with particular emphasis on generating finishing herd-specific profiles for carcass traits across different ages at slaughter. The data analysed in chapter 3 was from animals slaughtered in UK abattoirs. Genetic and finishing-herd-year of slaughter parameters were generated using random regression analysis. Across slaughter age and gender, the proportion of phenotypic variance accounted for by finishing-herd-year of slaughter variance was between 30.83%-71.48% for carcass weight, 21.38%-26.29% for conformation score and between 10.88%-44.04% for fat score. These parameters indicate that the finishing herd environment is an at least equally important contributor to carcass trait variability as the genetic background of animals, and amenable to improvement with appropriate management practices.

The final study of the thesis was to investigate the feasibility of across-country carcass trait genetic evaluations. Examination of the level of genetic connectedness between Ireland and the UK found 225 distinct bulls common to both countries. These common bulls were related to 80,707 Irish and 23,162 UK animals with carcass records in each population. Genetic correlations for carcass traits between Ireland and the UK were almost unity, ranging from 0.92 ( $\pm 0.31$ ) for fat score to 0.96 ( $\pm 0.17$ ) for carcass weight, indicating that the carcass traits recorded in both countries

are genetically essentially equivalent. These strong genetic correlations between carcass traits in both countries enabled the direct pooling of carcass data for the purpose of across-country genetic evaluations (breeding value estimation). An increased rate of genetic gain for carcass traits per generation was predicted from across-country selection compared to within country selection ranging from 2% (conformation score in Ireland) to 33.77% (conformation score in the UK). This improved gain was primarily due to greater intensity of selection and somewhat more accurate estimated breeding values when carcass records and pedigree information from both countries were combined.

The results presented in this thesis demonstrate that routinely collected abattoir data in Ireland and the UK can be exploited to produce additional selection and on-farm management tools. The results also show that access to across-country carcass trait genetic evaluations would allow UK and Irish beef farmers to make more informed decisions on the selection of seed stock needed to increase genetic gain and profits.

Outcomes of this thesis pave the way to improvements in national carcass traits genetic evaluations in Ireland and the UK based on appropriate age at slaughter and also demonstrate the feasibility of across-country carcass trait genetic evaluations between Ireland and the UK. The scope for further areas of research includes the identification of specific management practices for optimal herd performance for carcass traits. Additionally, across-country carcass trait genetic evaluations based on random regression models across different ages at slaughter would also be of benefit to beef producers in Ireland and the UK. Finally, the viability of across-country genetic



evaluations for additional carcass traits, such as carcass cut weights should be explored.

## **Lay Summary**

The main revenue source for beef farmers worldwide is carcass value (carcass weight, conformation and fat score). In general, heavier, better conformed (muscular), lean carcasses are awarded premium grades at the abattoirs. The grade a carcass receives is related to a number of factors, such as the genetics (breed) of the animal and the environment in which it is reared. In order to improve the profitability of the herd, breeders need an accurate means of comparing and selecting the best animals to breed from. Beef producers also need information on how their farm management (environmental) practices affect the performance of their animals. For predictive purposes, both Ireland and the UK routinely assess the productivity of animals for carcass traits, to estimate the improvement in these traits by the use of particular animals in breeding programs. The primary purpose of these evaluations is to distinguish the elite breeding stock in the population. These evaluations may be enhanced through employing alternative methods of analysis and by incorporating more information on animals or relatives of animals. This increase in information can be achieved through countries pooling their data. Pooling data also means that farmers in each country will have an accurate means of comparing foreign and domestic bulls, therefore getting access to the best selection candidates.

Using information on beef carcasses from abattoirs in Ireland and the UK, this thesis makes use of advanced statistical techniques to generate tools for the enhancement of selection and management decisions at a national (within each country) and international (between countries) level. The results from this thesis show that the influence of the genetic make-up of an animal on carcass traits varies across age and that there is variation between breeding bulls in their growth profiles for

carcass traits. This means that the progeny of some bulls develop at different rates compared to the progeny of other bulls, therefore they will be ready for slaughter at different ages. Knowledge of individual sire growth profiles for carcass traits could help farmers identify the most profitable time at which to slaughter the progeny of particular bulls, leading to a more efficient use of farm resources.

This thesis also showed how data collected for the purpose of genetic evaluations for carcass traits can yield useful information for consideration in farm management practices. The herd environment plays a significant role in carcass trait performance across ages at slaughter and years of slaughter and this information is a useful indicator of management practices across time.

In addition to the enhancement of within country evaluations, this thesis shows the potential benefits of an international evaluation for carcass traits. Access to international evaluations would allow Irish and UK beef farmers to make more informed decisions on the selection of seed stock needed to increase genetic gain in carcass traits.

These findings can now be used to develop breeding programmes which employ the best breeding stock and management practices to improve the performance and profitability of the herds within Ireland and the UK.

**List of Abbreviations**

|        |  |
|--------|--|
| ADG    | Average Daily Gain                           |
| AHDB   | Agriculture & Horticulture Development Board |
| AI     | Artificial Insemination                      |
| AIC    | Akaike's Information Criterion               |
| BASCO  | Beef and Sheep Breeding Company              |
| BLCS   | British Limousin Cattle Society              |
| BLUP   | Best Linear Unbiased Prediction              |
| BSE    | Bovine Spongiform Encephalopathy             |
| CV     | Coefficient of variation                     |
| d      | Days   |
| EBV    | Estimated Breeding Value                     |
| EGENES | Edinburgh Genetic Evaluations Services       |
| EU     | European Union                               |
| GxE    | Genotype by Environment                      |
| $h^2$  | Heritability                                 |
| Het    | Heterosis                                    |
| ICAR   | International Committee for Animal Recording |
| ICBF   | Irish Cattle Breeders Federation             |
| Kg     | Kilogrammes                                  |
| MACE   | Multiple-Trait Across Country Evaluation     |
| mm     | Millimeters                                  |
| Rec    | Recombination loss                           |
| RR     | Random Regression                            |
| RRM    | Random Regression Models                     |
| s.d.   | Standard deviation                           |
| SE     | Standard Error                               |
| SRUC   | Scotland's Rural College                     |
| UK     | United Kingdom                               |
| USA    | United States of America                     |
| VIA    | Video Image Analysis                         |

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# Chapter 1: General Introduction

## **1.1 Beef production**

### **1.1.1 Global beef production**

Beef production worldwide has more than doubled since the 1960s (Thornton, 2010) with the number of cattle increasing to approximately 25 million by the mid 2000s (Thornton, 2010). Of the approximately 60 million metric tonnes of beef produced worldwide in 2016, the United States of America (USA) were the largest producers (18.83%, followed by Brazil (15.35% and the European Union (EU) (12.98%) (Cook, 2017). Globally the beef industry is facing many challenges such as maintaining economic and environmental sustainability while concurrently fulfilling increased global food demands (Herd and Bishop, 2000). The world population is estimated to increase to 9.1 billion people by 2050 (Alexandratos and Bruinsma, 2012) coinciding with an increase in beef consumption of between 6% in developed countries and 21% in developing countries (OCED/FAO, 2016). As Ireland and the UK are significant producers of red meat, this increased global demand for beef may provide the Irish and UK beef industries with greater export opportunities.

### **1.1.2 Irish and UK beef production**

In Ireland and the UK, beef is derived from both the suckler and dairy herds. Beef production makes up 32% and 12% of Irish and UK agricultural output, respectively (EBLEX, 2012; DAFM, 2014). Considerable scope exists for growth within both these beef sectors. In 2016, beef and veal imports to the UK were approximately 400,000 tonnes whereas exports were 145,000 tonnes (AHDB, 2016). These export levels are still well below pre Bovine Spongiform Encephalopathy (BSE) levels despite the removal of the UK beef export ban in 2006. In contrast, Ireland is a net exporter of beef, exporting 70% (907,600 tonnes) of its total beef production in 2015, the majority

of which (52%) was to the UK (Forde, 2016). Ireland and the UK have been strong trading partners for generations. Of more recent concern to the beef industry in both the UK and Ireland are the implications of the UK's exit from the European Union (Brexit). The likely reduction or discontinuation of financial support for UK beef farmers could lead to a reduced level of production and greater reliance on imports, hindering the industry's efforts of achieving self-sufficiency (van Berkum et al., 2016). A possible increase in trade costs with Europe is also unfavourable, while the opening up of new trade routes outside of Europe may prove lucrative. From an Irish perspective, the potential increased cost of trade with the UK could reduce profitability as the majority of exported Irish beef (52%) is to the UK. Regardless of Brexit implications, the beef industry in both Ireland and the UK has a pressing need to increase efficiency, productivity and overall profitability.

### **1.1.3 Importance of beef carcass traits**

Among opportunities to increase profitability in the beef sector such as export development and better marketing, enhanced production methods have a fundamental role to play. The purchase of livestock and feed are among the largest costs for beef farmers (Arthur et al., 2001; Bertrand, 2001); therefore, increasing the quantity of beef output in a given time period by increasing individual animal performance could reduce costs and increase profit (Herd et al., 2003). This increased performance can be achieved through genetic selection for enhanced production traits such as feed conversion ratio (Arthur et al., 2001; Schenkel et al., 2004), weaning weight (Bennett & Gregory, 2001; Meyer, 2004), improved carcass traits (i.e., carcass weight, carcass

conformation and fat score) (Marshall, 1994; Gregory et al., 1995; Hickey et al., 2007), and increased growth rates.

Carcass value is fundamental to the profitability of beef farms (Bennett & Williams, 1998). This importance is reflected by the relative emphasis placed on carcass traits in selection indexes of both Ireland and the UK (Table 1.1 and Table 1.2). In Ireland and the UK, as in other European countries, the payment awarded for each carcass is based the overall carcass weight adjusted for the European Union EUROP classification system, which measures the overall carcass conformation and fat levels. This system assigns a conformation (i.e., the overall thickness of muscle in relation to the size of the animal's skeleton) and fat grade to each carcass. Conformation classification uses the letters E, U, R, O and P where E represents an excellent conformation and P represents a poor conformation. The fat classification system uses the scale 1, 2, 3, 4 and 5 where 1 represents a low fat composition and 5 a very high fat composition. Each conformation and fat class is further divided into 3 subclasses (+, =, -) (De Boer et al., 1974). A high proportion of muscle with an optimum level of fat cover characterise a superior carcass (Pesonen et al., 2012). Incorporation into breeding programmes of estimated breeding values (EBVs) for high value carcass traits facilitates selection based on carcass quality and production traits and can lead to a greater efficiency in meat production (Brackelsberg et al., 1971)..

## **1.2 Factors affecting beef carcass traits**

### **1.2.1 Genetic factors**

#### **1.2.1.1 Genetic parameters**

Carcass traits are biological characteristics of growth that exhibit genetic variability between animals (Bennett and Williams, 1998). The variability in carcass traits among

beef cattle is exemplified by the large number of studies in the literature reporting heritability estimates for carcass traits. Early carcass trait studies were generally carried out on smaller numbers of animals, from specialised research herds (Blackwell et al., 1962; Shelby et al., 1963; Koch et al., 1978; Splan et al., 2002). Efforts in the 1990's to increase the amount of carcass data available for carcass trait evaluations resulted in many studies investigating the use of live-animal ultrasound measurements of carcass traits in genetic evaluation programmes and the production of EBV's for proxy traits such as ultrasonic muscular and back fat measurements (Wilson, 1992; Moser et al., 1998; Crews, et al., 2001). Later studies explored the incorporation of routinely collected EUROP graded carcass records into genetic evaluation programmes. The advantage of using abattoir records for carcass trait genetic evaluations is that extremely large volumes of data are available compared to progeny testing or live animal experiments. In addition, abattoir records pertain to multiple breeds and carcass types from the commercial population where the genetic gain in carcass traits is needed most (Wall et al., 2013).

Regardless of how carcass traits were recorded, the majority of heritability estimates for carcass weight in the literature are moderate to strong (Koch et al., 1982; Reverter et al., 2000; Hickey et al., 2007). A review of carcass trait heritabilities by Rios-Utrera and Van Vleck (2004) reported an average age adjusted heritability estimate of 0.42 for carcass weight from data from 56 different studies. Nonetheless, heritability estimates as low as 0.10 (Wulf et al., 1996) and as high as 0.68 (Koch et al., 1978) have been reported in crossbred heifers and purebred Hereford heifers, respectively. Estimates of heritability for carcass conformation and fat traits in the literature are also moderate. For example, Eriksson et al. (2003) reported heritability

estimates for conformation between 0.26 and 0.39 and fat score between 0.23 and 0.45 in purebred young bulls. Similar ranges of conformation (0.24 to 0.44) and fat score (0.29 to 0.44) heritability estimates were also reported in purebred beef cattle by Kause et al. (2015). As with carcass weight, heritability estimates outside these ranges have also been reported. Gregory et al. (1995) reported a strong heritability estimate of 0.65 for conformation in purebred and crossbreed steers, whereas, Hickey et al. (2007) reported a carcass conformation heritability of 0.10 and a fat score heritability of 0.40 for Simmental x dairy and Hereford x dairy cattle, respectively.

Genetic studies of carcass traits using large volumes of routinely collected abattoir data are not as abundant in the literature as other carcass trait studies, but, of the studies available that use abattoir data, heritability estimates for carcass traits are moderate to strong (Reverter et al., 2000; Eriksson et al., 2003; Kause et al., 2015). Eriksson et al. (2003) reported heritabilities between 0.31-0.41 for carcass weight, 0.21-0.39 for conformation score and 0.23-0.45 for fat score in the progeny of Charolais, Hereford and Simmental sires. These carcass trait heritability estimates are within the ranges of those reported in studies from commercial cattle in UK and Irish populations. Hickey et al. (2007) reported varying direct heritability estimates for carcass weight in Irish cattle depending on breed composition, (0.17 for Aberdeen Angus or Belgian Blue sired to 0.65 Simmental sired). Pabiou et al. (2011), using data from Irish abattoirs, reported direct heritability estimates for EUROP graded conformation and fat score ranging from 0.28 to 0.46 and from 0.27 and 0.40, respectively, from an animal linear mixed model.

In general, the heritability estimates for carcass traits in the literature are within the ranges of those reported for live weight traits in beef cattle and many studies have

found an association between live weight measurements and carcass traits. Heritabilities of 0.45 and 0.47 were reported by Dodenhoff et al. (1998) for weaning weight and yearling weight, respectively, in Hereford cattle. Szabo et al. (2012) reported varying direct heritability estimates for weaning weight in cattle depending on breed (0.18 for Aberdeen Angus and 0.61 for Hungarian Grey sired). Blackwell et al. (1962) documented strong genetic correlations between weaning and yearling weights with carcass weight (0.70) and weaker correlations between weaning and yearling weights with ribeye area (0.29). Ultrasonic back-fat and muscle depth measurements are also moderately to strongly correlated with abattoir carcass trait measurements (Moser et al., 1998; Reverter et al., 2000; Devitt and Wilton, 2001). Crews et al., (2003) examined the genetic correlations between carcass traits and ultrasound measurements of fat thickness and longissimus muscle area in Simmental cattle. Genetic correlations of carcass fat thickness to ultrasonic fat measurements ranged between 0.79 ( $\pm 0.13$ ) and 0.83 ( $\pm 0.12$ ), depending on gender. Genetic correlations of carcass longissimus muscle to ultrasound longissimus muscle area were 0.80 ( $\pm 0.11$ ) and 0.54 ( $\pm 0.12$ ) for bulls and heifers, respectively. The positive correlations reported by Crews et al. (2003) between carcass traits and ultrasonic measurements were similar to correlations of carcass traits to ultrasonic measurements in previous studies (Moser et al., 1998; Wilson et al., 1999). The use of ultrasonic technology to measure body composition of live animals was a cost-effective and accurate means of gaining measurements on breeding animals (Robinson et al., 1993).

Since carcass trait phenotypes on which beef producers are paid are influenced by the genetic makeup of the animal, genetic improvement in carcass traits is important for increased production efficiency and increased profit (Wilton and Goddard, 1996).



The carcass trait genetic variances and associated genetic correlations between traits reported in the literature are of sufficient magnitude to be selected upon and are therefore responsive to genetic improvement through improved breeding decisions.

### **1.2.1.2 Genetic improvement**

Since the domestication of animals more than 12,000 years ago, humans have been making selection decisions for the improvement of livestock by breeding the most productive individuals (Lush, 1943). Until the mid-20<sup>th</sup> century, genetic progress was slow; however, the introduction of quantitative genetics techniques led to a large increase in genetic gain in production traits such as milk yield (Hill, 2010). Most traits of economic importance in agriculture are complex traits, controlled by a large number of genes (each having a small effect) and by environmental factors (Dekkers and Hospital, 2002). Selection methods based on quantitative genetics techniques involves the statistical analysis of phenotypic data combined with pedigree information to produce EBVs (EBVs are measures of the genetic potential of an animal for recorded traits). EBVs are mainly calculated with models yielding Best Linear Unbiased Predictions (BLUP), a method developed by Henderson in the 1950's. EBVs are used to rank available candidates for selection as parents of the next generation, so that the genetically superior animals are identified for breeding (Henderson, 1975). Genetic improvement in livestock is cumulative, permanent and cost effective and is achieved through applying this principle across several generations (Simm, 1998).

Genetic progress is well evidenced in the USA Holstein dairy population where the average milk yield has increased from approximately 6,000 kg per lactation in 1960 to almost 12,000kg per lactation in 2000; half of this increase is attributable to genetic improvement (Dekkers and Hospital, 2002). Increasing productivity through

genetically improving carcass traits has been well documented in many livestock species including chickens (Havenstein et al., 2003) and pigs (Filho et al., 2005). Havenstein et al. (2003) reported that up to 90% of gains in performance of broiler chickens since the 1960's is due to improvement genetics (Havenstein et al., 2003). Over a similar time period, improvements in pig breeding has led to a 40% increase in daily gain and a 35% decrease in back fat thickness (Merks, 2000).

Some genetic progress in beef cattle growth (Sullivan et al., 1999) and carcass traits have been demonstrated where selection has generally resulted in heavier, leaner carcasses (Arango and Vleck, 2002). Although significant amounts of genetic variance for carcass traits in cattle exists, the rate of genetic gain in beef carcass traits has been lower than that of carcass traits in other species possibly due to the large generation interval of cattle (Thornton et al., 2010). Also genetic improvement in carcass traits has been hampered by a lack of sire recording, discontinuity between pedigree and commercial breeders, and a lack of information on the carcass traits of breeding animals as these are an end-of-life traits and only accurately measured after slaughter (Evans et al., 2007; Pabiou et al., 2009).

Efforts to genetically improve beef cattle have been approached from a number of aspects such as genetic selection for increased growth weights (e.g. birth weight, weaning weight, and mature weight), greater calving ease or improved fertility traits (Meyer et al., 1992; Bertrand et al., 2001; Phocast and Sapa, 2004).

With regards to the genetic improvement of beef carcass traits, breeders often aim to genetically improve carcass traits by selecting on easier to measure correlated live weight traits (described in section 1.2.1.1). The amount of genetic gain in carcass traits in the commercial population achieved through selecting on correlated traits is

limited as most of the studies examining the relationship between growth and carcass traits were carried out within breed or on small populations of cattle from research herds (Riley et al., 2002; Rios-Utrera et al., 2005).

### **1.2.2 Management factors**

Carcass trait phenotypes are not only influenced by the genetic make-up of the individual animal but also by environmental factors such as the herd in which these animals are reared (Koch et al., 1982; Robinson et al., 1993; Elzo et al., 1998); therefore environmental influences on carcass traits should be appropriately evaluated and quantified. The need to improve beef carcass value, not only through improved genetic merit but also through improved production management systems has also been identified (Marshall, 1994; Pabiou et al., 2009). In other livestock species, the improved production levels seen since the 1960's are due to improved environmental factors such as management and nutrition in addition to improved genetics (Oltenacu et al., 2010; Havenstein, 2003).

Much research into the effect of management on beef production has been concerned with the effects of weaning management systems on performance (Peterson et al., 1987; Makarechian et al., 1988; Myers et al., 1999). In general, early weaning management systems result in heavier calves at the time that normal weaning would have occurred and also in younger, heavier animals at slaughter (Fluharty et al., 2000). Myers et al. (1999) examined the influence of weaning management on performance of British and continental breeds; they reported that earlier weaning (< 152 days) improved feed efficiency and improved carcass grades in beef steers. Story et al. (2000) also reported heavier slaughter weights in earlier weaned calves (150) as opposed to those weaned at normal ages (210 days) or later ages (270 days), but

emphasized that the profit potential of an early weaning system is affected by additional feed costs and other factors such as the time of year when steers are sold or finished.

Beef herd management practices for finishing cattle are usually evaluated at a systems level (e.g., intensive, semi-intensive, extensive) and a number of studies have examined the influence of finishing system on traits such as feed efficiency (Sami et al., 2004), carcass characteristics (Keane and Allen, 1998) or meat quality (Vestergaard et al., 2000; Priolo et al., 2002). Management evaluations at the herd level are generally lacking, possibly due to the low levels of on-farm recording among beef farmers. A large number of beef farms in Ireland and the UK are managed on a part-time basis (Mazurek et al., 2010); therefore, the financial and time resources needed to invest in on-farm recording is often not available. The management of beef cattle for slaughter generally consists of altering the penning and feeding arrangements of animals based on breed, gender or age.

In contrast to beef farming, dairy farming is generally a full time enterprise and on-farm recording is an integral part of management where it can be used as an indicator of health or nutritional status of the herd (Barkema et al., 1998; Heringstad et al., 2000). Many studies on dairy production have attempted to quantify the influence of individual herd management on lactation profiles by including a random herd effect in analyses to produce herd-specific trait profiles (Koivula et al., 2007; Caccamo et al., 2008; Bastin et al., 2009). These herd-specific trait profiles provide information on how animals within a herd perform compared to their expected performance under average management conditions (Caccamo et al., 2008) and have been incorporated into easy to use web tools (Koivula et al., 2007). Access to management tools for herd

performance for carcass traits (similar to dairy herd specific profiles discussed above) would be extremely beneficial to beef farmers.

### **1.3 Current state-of-the-art in the genetic evaluation for beef carcass traits**

#### **1.3.1 Ireland national genetic evaluations**

Until the mid-1990's beef selection methods were primarily based on phenotypes. Vast developments in the Irish data recording systems have come about over the past two decades. The formation of the Irish Cattle Breeders Federation (ICBF) in 1997 led to great improvements in the quality and quantity of data available to cattle breeders (Wickham & Durr, 2011). The information infrastructure has changed to a more streamlined supply chain structure with an integrated database and an associated genetic evaluation system. A major change was the implementation of an "Animal Events" on-farm recording system which allows farmers to enter calving related data and pedigree information. In 2010, the ICBF database stored information from 77,000 herds, representing 90% of the Irish cattle herd (Wickham & Durr, 2011) and by 2012, it contained approximately 28,000,000 records from a variety of sources (e.g. (Artificial Insemination (AI) companies, Farm recordings, Slaughter houses) (Lynch, 2012). These developments are of fundamental importance to Ireland's participation in international evaluations (discussed later).

Irish genetic evaluations are published in the form of a Euro-Star index and incorporate EBVs with the economic value of the trait to produce a monetary value of how profitable a sire's progeny are expected to be compared to the base animal. Euro-Star values are based on a scale of 1-5, each star representing an interval covering 20% of the population (ICBF, 2013). At present, the carcass traits evaluated are carcass

weight, conformation and fat score. Conformation and fat score are measured using Video Image Analysis (VIA).

The two Irish beef breeding objectives are the terminal and maternal selection indexes (combination of EBVs weighted to produce a single index value) and focus on farm level profitability (Amer et al., 2001). The terminal index is used when selecting sires to produce animals intended for slaughter and the maternal index used to breed for replacement females. Table 1.1 describes the national breeding objectives for beef cattle in Ireland; the genetic evaluations are undertaken across breed. The breeding objectives have a positive weight on carcass weight and conformation score and a negative economic weight on fat score (Berry, 2014).

**Table 1.1 Relative emphasis (weights) on traits in the Irish national beef maternal and terminal breeding objectives**

| Animals             | Trait  | Maternal<br>(€ per progeny<br>born) | Terminal<br>(€ per<br>progeny<br>born) |
|---------------------|--|-------------------------------------|--|
| All progeny         | Direct calving difficulty (%)                | -2.4                                | -20.5                                  |
|                     | Direct gestation length (days)               | -0.4                                | -3.7                                   |
|                     | Direct perinatal mortality (% dead at birth) | -0.4                                | -3.7                                   |
| Slaughtered progeny | Docility (points)                            | 0.3                                 | 2.4                                    |
|                     | Feed intake (kg)                             | -2.2                                | -18.8                                  |
|                     | Carcass weight (kg)                          | 3.5                                 | 35.8                                   |
|                     | Carcass conformation (points)                | 1.1                                 | 9.5                                    |

|   |  |      |      |
|---|--|------|------|
|   | Carcass fat (points)                         | -0.6 | -5.6 |
|   | Age at first calving (days)                  | -5   |      |
|   | Maternal calving difficulty (%)              | -4.5 |      |
|   | Maternal weaning weight (kg)                 | 12.4 |      |
| Replacement progeny                                     | Calving interval (days)                      | -7   |      |
|   | Cow survival (%)                             | 5    |      |
|   | Heifer feed intake (kg)                      | -7.7 |      |
|   | Cow feed intake (kg)                         | -7.4 |      |
|   | Cow docility (points)                        | 2.9  |      |
|   | Cull cow weight (kg)                         | 5.5  |      |
|   | Direct calving difficulty (%)                | -8.8 |      |
|   | Direct gestation length (days)               | -1.6 |      |
| Slaughtered progeny from female replacement descendants | Direct perinatal mortality (% dead at birth) | -1.6 |      |
|   | Docility (points)                            | 1    |      |
|   | Feed intake (kg)                             | -5.7 |      |
|   | Carcass weight (kg)                          | 8.7  |      |
|   | Carcass conformation (points)                | 2.7  |      |
|   | Carcass fat (points)                         | -1.6 |      |

### 1.3.2 UK national genetic evaluations

EBVs were introduced into the UK beef industry in the mid-1990's, following almost two decades of genetic progress in the dairy industry (Crumps et al., 2010). Beef EBVs were originally calculated for just growth and live carcass traits (live weight and ultrasound measurements of back fat and muscularity) and from the mid 2000's evaluations were expanded to include female fertility traits (Roughsedge et al., 2005). The data used in the evaluations was mainly pedigree records and farmer recorded phenotypes, but large volumes of abattoir recorded phenotypes (carcass weight, conformation & fat scores) are now available for inclusion in the national carcass trait evaluations. The UK publish individual trait EBVs and also publish selection indexes.

The UK beef breeding objectives include fertility traits, carcass quality traits and weight traits. The indexes currently available to UK beef breeders are; Beef Value, Calving Ease, Maternal Value and Maternal Production Value which is a combination of the previous three (Coffey et al., 2007). Table 1.2 describes the weightings for traits included in the relative indexes for the Limousin breed (personal communication BLCS, 2014). The UK Limousin beef value index has a negative weighting on early live weight and a positive weighting on live weight at older ages and, similar to the Irish terminal selection index, has a positive weighting on muscle depth and a negative weighting on fat depth.

Accurate evaluations rely on large quantities of phenotypic records including pedigree information. Performance recording in the UK has undergone substantial changes in recent years with the merging of data sources and the accumulation of records. The formation of the Beef and Sheep Company (BASCO) by the joining of the three largest beef and sheep breed societies in the UK (British Limousin Society, Suffolk Sheep Society and British Texel Sheep Society) has led to improvements in information transfer between pedigree breeders and societies and has improved the efficiency of performance recording and genetic evaluations in the beef and sheep industries (Coffey et al., 2007). For the majority of UK beef cattle, evaluations are provided via Edinburgh Genetic Evaluations Services (EGENES) in collaboration with BASCO and the Agriculture and Horticulture Development Board Beef and Lamb (AHDB Beef and Lamb), the organisation for beef and lamb levy payers in England. The Limousin society independently contracts EGENES to carry out their evaluations. Unlike Ireland, who have been publishing VIA conformation and fat scores in routine



genetic evaluations since 2009, EUROP graded carcass trait EBV's are currently not available to UK beef breeders.

**Table 1.2 Relative emphasis (weights) on traits in the UK beef breeding objectives (Limousin breed)**

| Index description | Trait included in index     | Weighting of trait<br>(£ per progeny born) |
|-------------------|-----------------------------|--|
| Beef value        | Birth weight (kg)           | -5.2                                       |
|                   | 200 day weight (kg)         | -0.6                                       |
|                   | 400 day weight (kg)         | 0.7  |
|                   | Muscle score (mm)           | -1.3                                       |
|                   | Fat depth (mm)              | -0.5                                       |
|                   | Muscle depth (mm)           | 3.7  |
|                   | Gestation length (days)     | 1.4  |
|                   | Calving ease direct (%)     | 15.8                                       |
| Calving value     | Gestation length (days)     | -1.0                                       |
|                   | Calving ease direct (%)     | -7.1                                       |
| Maternal value    | Calving interval (days)     | -0.8                                       |
|                   | Age at first calving (days) | 48.1                                       |
|                   | Life span (days)            | 6.6  |

|                           |                              |       |
|---------------------------|------------------------------|-------|
|                           | Maternal 200 day weight (kg) | 0.7   |
|                           | Maternal calving ease (%)    | 2.2   |
| Maternal Production value | 400 day weight (kg)          | -0.1  |
|                           | Muscle score (mm)            | 7.9   |
|                           | Fat depth (mm)               | 3.1   |
|                           | Muscle depth (mm)            | 1.3   |
|                           | Gestation length (days)      | -1.2  |
|                           | Calving ease direct (%)      | 1.3   |
|                           | Calving interval (days)      | -0.8  |
|                           | Age at first calving (days)  | -48.1 |
|                           | Life span (days)             | 6.6   |
|                           | Maternal 200 day weight (kg) | 0.7   |
|                           | Maternal calving ease (%)    | 2.2   |

---

### **1.3.3 International evaluations**

Herd sizes in the UK and Ireland tend to be small, therefore restricting the choice of animals to select as breeding animals and limiting the rate of genetic progress. Furthermore beef cattle breeding is now an international business due to the sale of seed stock across countries; with breeders wishing to choose from a larger pool of candidates best suited to their breeding goals (Phocas et al., 2005). There is therefore a need for accurate national evaluations as a method of comparison between animals of different herds and the need of international evaluations as a means of comparing animals between countries (Ahlqvist, 2010).

The accuracy of genetic evaluations can be improved by pooling data thereby increasing the quantity of data available for individual animals or their relatives. The pool of selection candidates can be increased by having access to accurate information on international selection candidates (Banos and Sigurdsson, 1996). Therefore international evaluations would allow beef farmers worldwide to make more informed decisions on the selection of seed stock needed to increase genetic gain and profit (Wickham and Durr, 2011).

Across-country genetic evaluations have been undertaken in dairy cattle by Interbull since the mid-nineteen nineties and have resulted in a large increase in genetic gain (Brotherstone and Goddard, 2005). Issues for consideration in across-country genetic evaluations include data validation, model selection, genetic connectedness among populations in different countries and genotype by environment (GxE) interactions (Fouilloux et al., 2006; Venot et al., 2007). GxE interactions mean that genotypes respond differently to changes in the environment (Kolmodin et al., 2002). The presence of GxE interactions may result in the re-ranking of sires between countries (Renand et al., 2003) and reduce the efficiency of selection programmes (Goddard and Hayes, 2007). Having duly considered the above issues, Interbull determined that a linear multiple-trait across country evaluation (MACE), where the dependant variable is de-regressed proofs (Banos and Sigurdsson 1996) was best suited for the purpose of across-country genetic evaluations in dairy cattle. Prior to the application of mixed models for across-country evaluations of sires, conversion equations were used to evaluate sires from foreign countries, which are much inferior to MACE (Sullivan et al., 2005). In MACE, progeny contributions from different countries are treated as different traits, with genetic correlations of less than unity allowed (Schaeffer, 1994).

The identification of superior beef animals across countries to be used as breeding parents is the reasoning behind the establishment of the International Beef Evaluations (Interbeef), which set out to facilitate accurate and widespread across-country evaluations of beef traits. Interbeef is a working group of the International Committee for Animal Recording (ICAR), which is an international standards body for the livestock industry. To date much of the focus of Interbeef has been on across-

country genetic evaluations for weaning weights, with official international EBVs for weaning weights having been shared with participating countries. A multi-trait animal model is also used by Interbeef for across-country weaning weight evaluations. Unlike across-country dairy evaluations, the dependent variable is adjusted weaning weight phenotypes. The across-country weaning weight evaluation model proposed by Phocas et al., (2005) accounts for heterogeneous variation between countries and allows the prediction of international EBVs for all animals in the pedigree (Phocas et al., 2005; Venot et al., 2007).

Interbeef have been primarily concerned with across-country genetic evaluations of purebred beef cattle (Limousin and Charolais). However, availability of across-country genetic evaluations for multiple breeds including crossbreds would better serve the breeding goals in beef-producing countries by increasing the rate of genetic improvement of the commercial beef herd, which in turn would have a positive impact on both the efficiency and profitability of farms. A survey carried out by Interbeef to determine traits of interest for international genetic evaluations found that all participating countries had a high interest in including carcass weight and conformation in these evaluations (Forabosco et al., 2009). Currently, however, no official international genetic evaluations for carcass traits exist and the work from this PhD will feed into the global carcass trait evaluations initiative.

#### **1.4 Scope beyond state-of-the-art**

In the BLUP procedure, carcass traits are adjusted by age at slaughter, and therefore, for each animal that is older or younger than the mean age at slaughter there will be a phenotypic trait correction (Robinson et al., 1991). Carcass traits, however, develop over the lifetime of an animal. Potentially there are different genes turned on or off as

the animal ages causing changes in physiology or performance over time, and therefore, carcass traits at different ages may be considered to continuously vary over time (Wilson et al., 2005).

An appropriate technique for analyzing traits that change across a time trajectory (such as all possible slaughter ages) is random regression analysis (Meyer, 1999). Random regressions were first applied to animal breeding by Henderson (1982) and have since been applied to the study of longitudinal data in many species such as live weight in pigs (Huisman et al., 2002), body weight in fish (Rutten et al., 2004); milk yield in dairy goats (Mucha et al., 2014); and are now routinely used in the genetic evaluation of production traits in dairy cattle (Ptak and Schaeffer 1993; Bohmanova et al., 2008). Random regression analyses facilitate the estimation of genetic parameters and EBV's for all time points across a trajectory (Schaeffer, 2004). Knowledge of the genetic potential of animals for carcass traits across all possible ages at slaughter may help producers make more informed selection decisions.

Even though national genetic evaluations for carcass traits are well established, the absence of formal herd or environmental evaluations for carcass trait performance has slowed the phenotypic improvement in carcass traits. In traditional carcass trait genetic evaluations using linear animal models, carcass traits are adjusted for average management conditions usually in the form of fixed finishing herd-year of slaughter-season of slaughter contemporary groups. Fitting management groups as fixed allows breeders to compare genetic differences (EBV's) of sires across herds (Van Groningen et al., 2006). Although useful, fitting herd effects as fixed does not provide information on individual herd performance across time. Knowledge of how the individual herd

environment influences beef carcass characteristics across ages at slaughter would help farmers make more informed on-farm management decisions.

In order to achieve maximum improvement in carcass trait performance, beef breeders need access to the most elite breeding stock. Across-country genetic evaluations which facilitate the direct comparison of bulls between countries have had beneficial effects on the rate of genetic gain in production traits in dairy cattle (Brotherstone and Goddard, 2005). Information on across-country genetic evaluations for carcass traits may help improve selection decisions by Irish and UK beef breeders by increasing the pool of selection candidates for both countries.

## **1.5 Objectives and thesis outline**

This PhD aims to generate novel tools, knowledge and information for the enhancement of national and international genetic evaluations of carcass traits in beef cattle by:

1. Modelling genetic effects on carcass traits across different ages at slaughter in order to improve genetic selection tools.
2. Modelling herd effects on carcass traits across different ages at slaughter after adjustment for genetic effects in order to facilitate on-farm management practices.
3. Exploring the benefits of across-country genetic evaluations for the three carcass traits, carcass weight, conformation and fat score.

Chapter 2 concerns the modelling of carcass data for the development of sire genetic growth profiles, thereby providing more informed tools for genetic selection.

Chapter 3 demonstrates the use of carcass data for the purpose of providing information on herd performance and the development of herd management tools, which is complementary to information produced on the genetic merit of animals (Chapter 2).

Chapter 4 assesses the feasibility of and benefits from an across-country genetic evaluation between Ireland and the UK for beef carcass traits using routinely collected abattoir data from the two countries.

## **Chapter 2: Genetic analysis of carcass traits in beef cattle using random regression models**



## **2.1 Chapter introduction**

Commercially collected abattoir data is routinely analysed to derive genetic evaluations of carcass traits for the purposes of genetic selection with the ultimate goal of increasing genetic gain. Currently carcass trait genetic evaluations are based on conventional BLUP methodology. This chapter explores an alternative approach to genetic evaluations of beef cattle sires using random regression techniques and a time trajectory defined by the slaughter age of the sires' progeny. In addition to producing EBVs for carcass traits across this time trajectory, the chapter also demonstrates how these EBVs can be incorporated into valuable selection tools in the form of individual sire growth profiles. Results address the first objective of this thesis. The body of the chapter has been published in the Journal of Animal Science.

The student conducted all the work related to this chapter under guidance from her supervisors and in collaboration with the remaining authors of the manuscript.

## 2.2 Manuscript

### Genetic analysis of carcass traits in beef cattle using random regression models

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### ABSTRACT

Livestock mature at different rates depending in part on their genetic merit; therefore, the optimal age at slaughter for progeny of certain sires may differ. The objective of the present study was to examine sire-level genetic profiles for carcass weight, carcass conformation and carcass fat, in cattle of multiple beef and dairy breeds, including crossbreeds. Slaughter records from 126,214 heifers and 124,641 steers aged between 360 and 1200 days, and from 86,089 young bulls aged between 360 and 720 days, were used in the analysis; animals were from 15,127 sires. Variance components for each trait across age at slaughter were generated using sire random regression models that included quadratic polynomials for fixed and random effects; heterogeneous residual variances were assumed across ages. Heritability estimates across genders ranged from 0.08 ( $\pm$  0.02) to 0.34 ( $\pm$  0.02) for carcass weight, 0.24 ( $\pm$  0.02) to 0.42 ( $\pm$  0.01) for conformation and 0.16 ( $\pm$  0.03) to 0.40 ( $\pm$  0.02) for fat score. Genetic

correlations within each trait across ages weakened as the interval between ages compared lengthened, but were all  $>0.64$  suggesting a similar genetic background for each trait across different ages. Eigenvalues and eigenfunctions of the additive genetic covariance matrix revealed genetic variability among animals in their growth profiles for carcass traits although most of the genetic variability was associated with the height of the growth profile. At the same age, a positive genetic correlation (0.60 to 0.78; standard errors ranged from 0.01 to 0.04) existed between carcass weight and conformation, whereas negative genetic correlations existed between fatness and both conformation (-0.46 to 0.08; standard errors ranged from 0.02 to 0.09) and carcass weight (-0.48 to -0.16; standard errors ranged from 0.02 to 0.14) at the same age. The estimated genetic parameters in the present study indicate genetic variability in growth trajectory in cattle which can be exploited through breeding programmes and used in decision support tools.

**Keywords:** cattle, carcass weight, conformation, fat, Legendre polynomials, random regression

## **INTRODUCTION**

Animals develop and mature at different rates depending on their genetic merit (Marshall, 1994; Robinson, 1996). Therefore progeny of some animals may reach the desired carcass weight, conformation, and subcutaneous fat level specified by abattoirs at different ages. As these traits are the most economically important in beef cattle production, knowledge of the optimum age at which an animal is likely to be suitable for slaughter is desirable. High heritability of various carcass characteristics in cattle have been documented (Hickey et al., 2007; Pabiou et al., 2011a) and thus genetic merit of the individual is likely to have a strong impact on such characteristics.

Random regression models (RRM) are widely used in the dairy industry to model lactation profiles (Jamrozik et al., 1998; Cobuci et al., 2005). Random regressions have also been used in the study of growth on a live weight basis, using multiple measures recorded over time (Meyer, 2001; Coffey et al., 2006). Random regression models have not, however, been used in the study of carcass traits since these are end-of-life traits measured only once in an animal's lifetime. It is, nonetheless, possible to longitudinally model a trait for different sires exploiting information on the relatedness among progeny slaughtered at different ages, thereby providing several effective measurements per sire across a time trajectory (Jonest et al., 1999).

The objective of the present study was to examine sire genetic profiles for three carcass traits namely carcass weight, carcass conformation and carcass fat across different ages of progeny slaughtered. Knowledge of the genetic variability in the trajectory for carcass traits could facilitate more informed selection and management decisions such as penning of animals with expected similar growth patterns.

## **MATERIALS AND METHODS**

All data used in the present study were obtained from the Irish Cattle Breeding Federation (ICBF) database.

### ***Data***

Carcass weight (kg), carcass conformation (scale 1 to 15; Table 2.1) and carcass fat score (scale 1 to 15; Table 2.1) records from 5,223,983 singleton animals from 101,171 Irish herds slaughtered between the years 2010 and 2013 were available. Carcass weight is measured on average two hours after slaughter following the removal of the head, legs, thoracic and abdominal organs, and internal fats and hide. In Ireland,

carcass conformation and fat scores are graded using Video Image Analysis (Pabiou et al., 2011b). The resulting EUROP classification grades were transformed into a 15-point numeric scale outlined in Table 2.1.

**Table 2.1** Numerical values on a 15-point scale in classification units given to carcass conformation class and carcass fatness class scores using a 15-, 7-, or 5-point scale.\*

| Conformation class scale    |               |               | Fatness class scale         |               |               |
|-----------------------------|---------------|---------------|-----------------------------|---------------|---------------|
| 15 point scale <sup>1</sup> | 5 point scale | Numeric value | 15 point scale <sup>2</sup> | 7 point scale | Numeric value |
| E+                          | E             | 15            | 5+                          | 5             | 15            |
| E=                          |               | 14            | 5=                          |               | 14            |
| E-                          |               | 13            | 5-                          |               | 13            |
| U+                          | U             | 12            | 4+                          | 4H            | 12            |
| U=                          |               | 11            | 4=                          |               | 11            |
| U-                          |               | 10            | 4-                          | 4L            | 10            |
| R+                          | R             | 9             | 3+                          |               | 9             |
| R=                          |               | 8             | 3=                          | 3             | 8             |
| R-                          |               | 7             | 3-                          |               | 7             |
| O+                          | O             | 6             | 2+                          |               | 6             |
| O=                          |               | 5             | 2=                          | 2             | 5             |
| O-                          |               | 4             | 2-                          |               | 4             |
| P+                          | P+            | 3             | 1+                          |               | 3             |
| P=                          | P-            | 2             | 1=                          | 1             | 2             |
| P-                          | P-            | 1             | 1-                          |               | 1             |

<sup>1</sup>E+ is the best conformation; P- is the worst conformation.

<sup>2</sup>5+ is the fattest; 1- is the leanest.

\* Hickey et al. (2007).

Records were removed for animals that moved herd more than once during their lifetime. The remaining 1,319,863 records were restricted to animals slaughtered >360 days or <1200 days of age. Cows (i.e., females that had at least one recorded calving date) and mature bulls >720 days of age at slaughter were not further considered, nor were animals with no recorded sire or dam. Furthermore, records more than four standard deviations from the within gender population mean carcass weight or age at slaughter were also discarded. Only carcass weight records between 120 kg and 543

kg, between 120 kg and 577 kg, and between 136kg and 577 kg were retained for heifers, steers and young bulls, respectively. Dam parity was restricted to 1 to 10 and parity was subsequently categorized as 1, 2, 3, 4, and  $\geq 5$ . Only progeny from sires with at least 5 paternal half-sibs with records were retained. Following these edits, 541,595 carcass records remained. Two contemporary groups were generated: 1) herd-year-season-gender of slaughter and 2) abattoir-date of slaughter. Gender in the present study refers to heifer, steer, or young bull. An algorithm was used to maximize the size of the herd-year-season-gender of slaughter contemporary group while simultaneously minimizing the duration of the contemporary group in time; this algorithm has been described in detail for genetic analyses of other animal traits in Irish genetic studies (McHugh et al., 2011; Berry and Evans, 2014). No contemporary group was longer than 60 days in duration and only contemporary groups with at least five records were retained. Following edits, 336,944 animals from 27,417 herd-year-season-gender contemporary groups in 9,572 herds remained. Of this dataset, 126,214 (37.5% of the data) were heifers, 124,641 (37% of the data) were steers and 86,089 (25.5% of the data) were young bulls. Animals included in the analysis were from 15,127 sires. The pedigree of each animal was traced back to founder populations which in turn were allocated to genetic groups. The pedigree file consisted of 88,324 animals.

### ***Data Analysis***

Variance components for carcass weight, conformation and fat score were estimated for each gender separately using sire RRM in AsReml (Gilmour et al., 2009). The data of young bulls were divided into nine groups based on age at slaughter as 360-400, 401-440, 441-480, ....., 681-720 days. Heifer and steer data was divided into 21 groups

as 360-400, 401-440, 441-480, ..., 1161-1200 days. Residual variances were assumed to be homogenous within each age class but heterogeneous between each age class.

The number of animals in each residual class is in Table 2.2.

**Table 2.2** Numbers of heifer, steer, and young bull records, in each residual variance class group.

| Class (days) | Heifers | Steers | Young Bulls |
|--------------|---------|--------|-------------|
| 360-400      | 566     | 162    | 1,399       |
| 401-440      | 1,293   | 374    | 3,979       |
| 441-480      | 1,937   | 582    | 8,051       |
| 481-520      | 2,790   | 753    | 9,724       |
| 521-560      | 4,700   | 1,293  | 10,288      |
| 561-600      | 7,791   | 1,936  | 12,316      |
| 601-640      | 11,202  | 3,058  | 13,083      |
| 641-680      | 16,414  | 6,460  | 13,405      |
| 681-720      | 20,151  | 13,113 | 13,844      |
| 721-760      | 17,552  | 19,681 | N/A         |
| 761-800      | 11,718  | 18,329 | N/A         |
| 801-840      | 8,069   | 13,202 | N/A         |
| 841-880      | 6,665   | 10,821 | N/A         |
| 881-920      | 5,719   | 12,096 | N/A         |
| 921-960      | 2,637   | 7,027  | N/A         |
| 961-1000     | 1,971   | 5,046  | N/A         |
| 1,001-1,040  | 1,575   | 3,742  | N/A         |
| 1,041-1,080  | 1,274   | 2,916  | N/A         |
| 1,081-1,120  | 991     | 2,137  | N/A         |
| 1,121-1,160  | 709     | 1,205  | N/A         |
| 1,161-1,200  | 490     | 708    | N/A         |

N/A= not applicable

The fitted model was

$$\begin{aligned}
 Y_{dhjklqnz} = & Parity_d + Abattoir - DoS_j + \sum_{h=1}^9 c_h . Dambreed_h \\
 & + a_1 . Het + a_2 . Rec + \sum_{i=1}^n b_n P_n Age + \sum_{i=1}^n Sire_{kn} P_n Age \\
 & + \sum_{i=1}^n HY_{ln} P_n Age + HYS_q + e_{dhjklqnz}
 \end{aligned}$$

(2.1)

where  $Y_{dhjklqnz}$  = the observed carcass weight, carcass conformation class or carcass fatness class on animal  $z$ ;  $Parity_d$  = the fixed effect of the  $d^{th}$  parity of the dam of animal  $z$  (5 levels);  $Abattoir-DoS_j$  = fixed effect of date of slaughter  $j$  (12,251 levels);  $c_h$  = partial regression coefficients on proportion of breed of the dam (Dambreed)  $h$  summed over all breeds (sum of proportion across the 9 breeds equals to unity);  $a_1$  = linear regression coefficients on heterosis (Het) in animal  $z$ ;  $a_2$  = linear regression coefficients on recombination loss (Rec) in animal  $z$ ;  $Age$  = age at slaughter;  $b_n$  = fixed regression coefficient on age at slaughter;  $P_n$  =  $n^{th}$  order Legendre polynomial of age at slaughter;  $Sire_{kn}$  = random regression coefficient on age at slaughter associated with the genetic effect of sire  $k$  of animal  $z$ ;  $HY_{ln}$  = random regression coefficient on age at slaughter associated with the effect of gender finishing herd-year of slaughter  $l$ ;  $HYS_q$  = the random effect of gender finishing herd-year-season of slaughter  $q$ ;  $n$  = the order of Legendre polynomial;  $e_{dhjklqnz}$  = the residual error term for age class modelled as heterogeneous across age.

The most parsimonious fixed effect Legendre polynomial regression was based on both the F-statistic of the higher order polynomial terms but also by visual comparison of the resulting profile for the different model orders. In all instances a quadratic fixed effect polynomial was most appropriate. Although a higher order polynomial fitted the data better ( $P < 0.05$ ), the profiles of the quadratic and higher order polynomials were visually identical. The decision of the most parsimonious order of random Legendre polynomial regression on sire was based on the Akaike's Information Criterion (AIC) with the fixed effects in the model being consistent across models compared.

Genetic covariance function coefficients were estimated as



$$\delta^2 = \Phi'K\Phi$$

where  $\delta^2$  is the variance (co)variance matrix for slaughter ages,  $\Phi$  is the matrix of Legendre polynomial age regression coefficients, and  $K$  is the estimated variance covariance matrix of the random polynomial coefficients multiplied by four to transform from a sire variance to a genetic variance (Huisman et al., 2002). Standard errors of the heritability estimates were derived using a Taylor series expansion (Fischer et al., 2004).

Genetic correlations between carcass weight, conformation and fat score at each age were estimated using a series of bivariate RRM analyses in AsReml (Gilmour et al., 2009). Fixed and random effects included in the models were as described for the univariate analyses (model 2.1). The inability of bivariate models to converge when a higher order of random regression was fitted necessitated the order of the fitted random regression to be linear. Residual variances were estimated within each age class as described for the univariate analysis, and a residual covariance between traits was assumed within residual age classes.

Standard errors of genetic correlations were estimated using (Falconer and MacKay, 1996):

$$\sigma_{(r_A)} = \frac{1 - r_A^2}{\sqrt{2}} \sqrt{\frac{\sigma(h_x^2) \sigma(h_y^2)}{h_x^2 h_y^2}}$$

where  $\sigma$  denotes the standard error,  $r_A$  is the genetic correlation between trait  $x$  and trait  $y$ , and  $h^2$  is the heritability; the superscript  $x$  or  $y$ , represent the respective traits under investigation.

Eigenvalues and eigenvectors were calculated from singular value decomposition of the additive genetic covariance matrix, and eigenfunctions were

subsequently calculated from the product of the eigenvectors and Legendre polynomial coefficients as:

$$\Psi_i(x) = \sum_{j=0}^{p-1} [k_{\psi_i}]_j \phi_j(x)$$

Where  $[k_{\psi_i}]_j$  is the  $j^{th}$  element of the  $i^{th}$  eigenvector of  $K$ ,  $\phi$  is the  $j^{th}$  polynomial relating to the  $p^{th}$  order of fit, and  $x$  is age of slaughter.

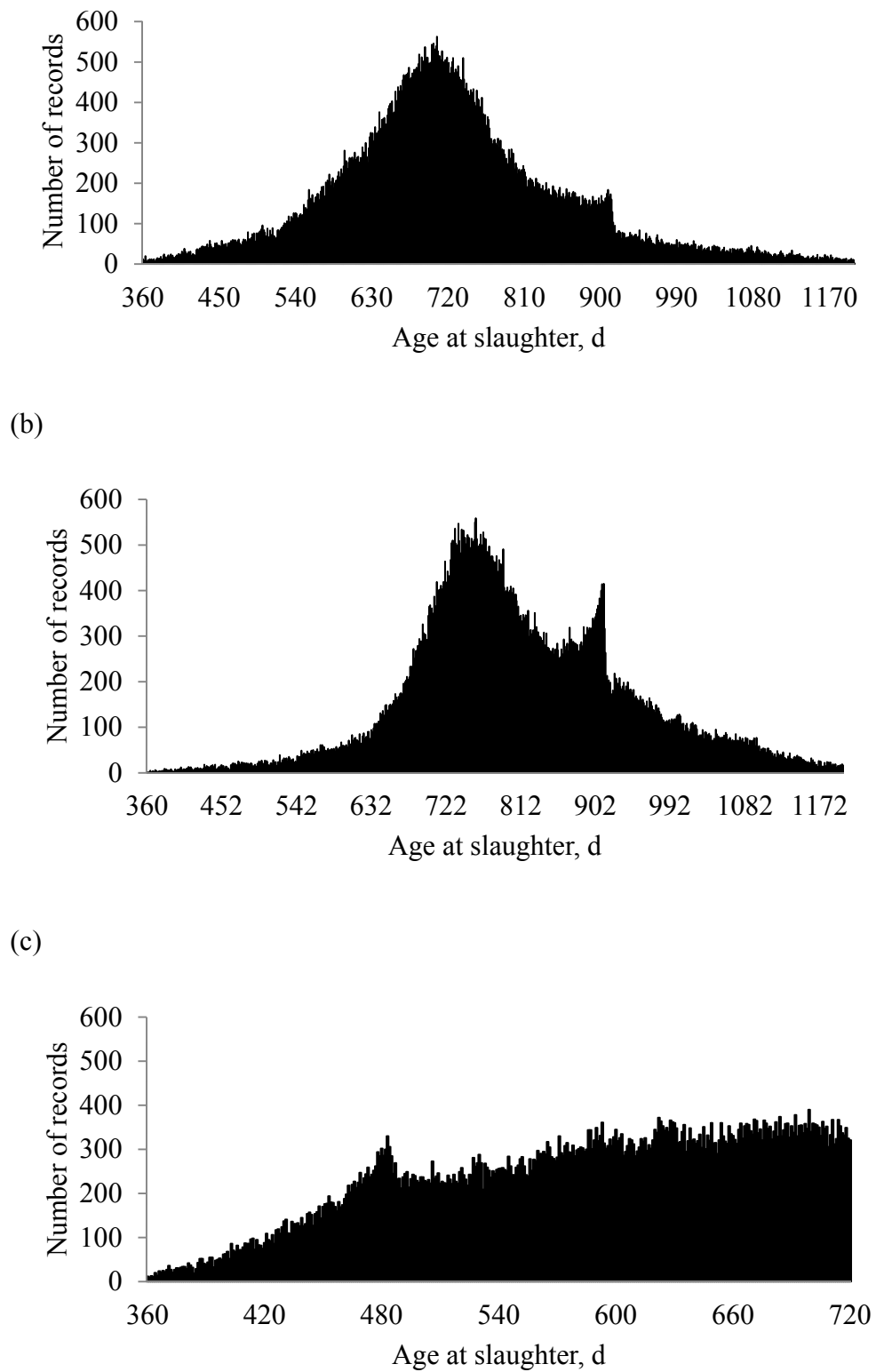
## RESULTS

The frequency distribution at age of slaughter for young bulls, steers and heifers is in Figure 2.1. Young bulls were slaughtered at an average age of 583 days and had a heavier mean carcass weight than steers and heifers. Young bulls also had the best conformation and were the leanest of the three genders. For all genders, carcass weight increased constantly as animals aged (Figure 2.2). Maximum conformation (i.e., age at point of inflection) was reached in steers and heifers at a similar age of 934 days and 938 days, respectively.

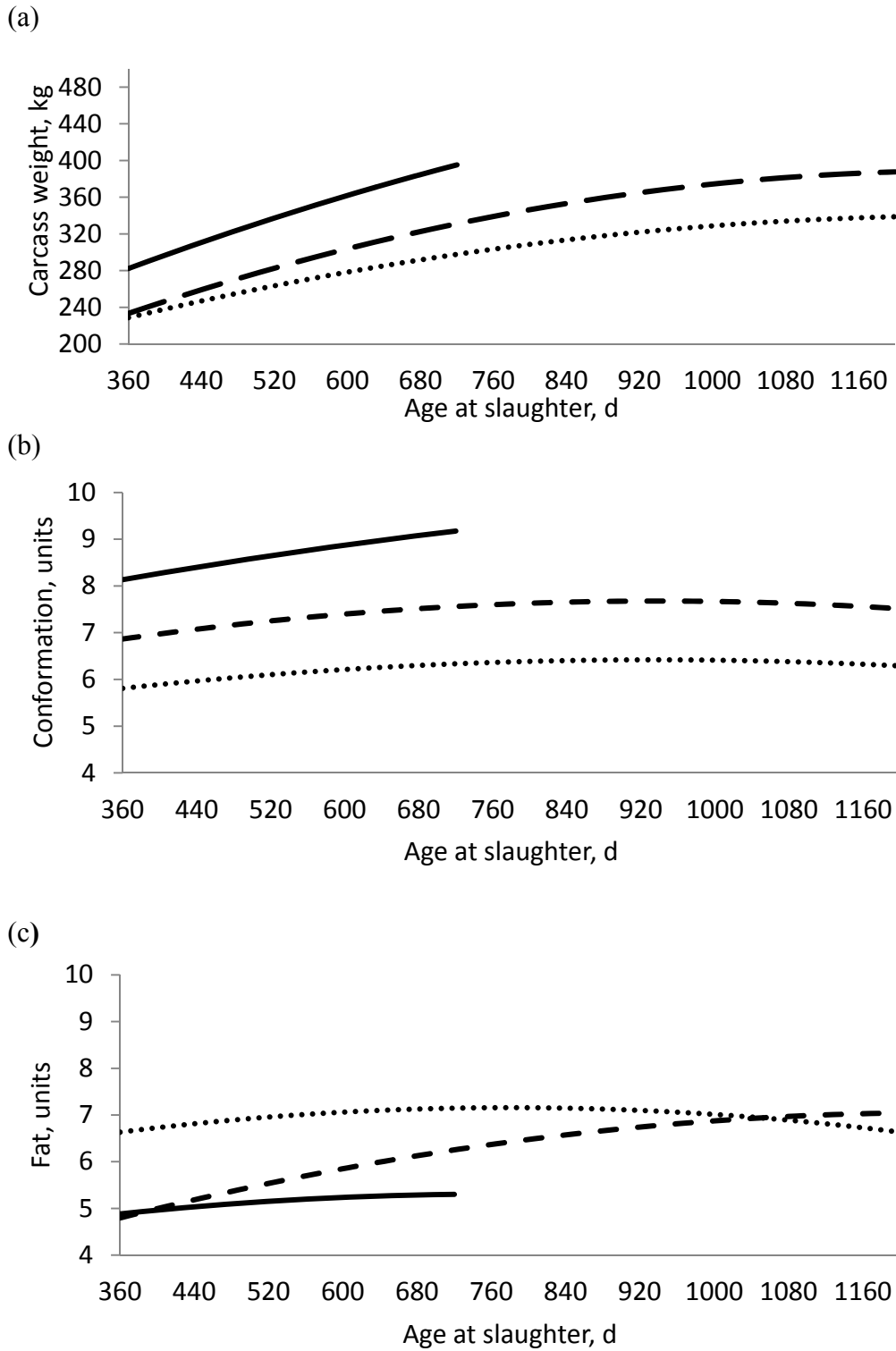
In young bulls and steers, fat deposition increased as age at slaughter increased albeit, at a declining rate, whereas fat deposition reached maximum in heifers at 780 days. A total of 96.6% per cent of the young bulls were slaughtered between the ages of 420 and 720 days. A total of 84.8% of steers were slaughtered between 650 and 1010 days of age. Of the heifers slaughtered, 84.3% were slaughtered between the ages of 530 and 900 days. Therefore, to minimize the influence of data at the extremities of the parameter space on the fitted polynomials at the extremes, only (co)variance components between 420 and 720 days, 650 and 1010 days and 530 and 900 days are presented for young bulls, steers and heifers, respectively.

Descriptive statistics of carcass weight, conformation score, fat score and age at slaughter in each gender are in Table 2.3. Young bulls were slaughtered at an average age of 583 days and had a heavier mean carcass weight than steers and heifers. Young bulls also had the best conformation and were the leanest of the three genders. For all genders, carcass weight increased constantly as animals aged (Figure 2.2). Maximum conformation (i.e., age at point of inflection) was reached in steers and heifers at a similar age of 934 days and 938 days, respectively. In young bulls and steers, fat deposition increased as age at slaughter increased albeit, at a declining rate, whereas fat deposition reached maximum in heifers at 780 days.

(a)



**Figure 2.1** Distribution of age at slaughter for (a) heifers, (b) steers, and (c) young bulls.



**Figure 2.2** Fixed effects profiles for (a) carcass weight, (b) carcass conformation, and (c) carcass fat for heifers (— — —), steers (· · ·), and young bulls (—), estimated using quadratic polynomials. The intercept was taken as the weighted average of contemporary group and abattoir-date of slaughter and fixed effects from a fifth-parity dam with no heterosis or recombination loss. Carcass conformation and fat scores were measured on a scale of 1 to 15.

**Table 2.3** Mean, standard deviation (s.d.) and coefficient of variation (CV) for each gender for each carcass trait and age at slaughter.

| Gender                  | Trait                     | Mean   | s.d.   | CV%   |
|-------------------------|---------------------------|--------|--------|-------|
| Heifers<br>n=126,214    | Carcass weight (kg)       | 297.65 | 45.27  | 15.20 |
|                         | Conformation <sup>1</sup> | 7.53   | 1.85   | 24.56 |
|                         | Fat <sup>2</sup>          | 7.26   | 1.85   | 25.48 |
|                         | Age at slaughter (days)   | 725.20 | 134.51 | 18.55 |
| Steers<br>n=124,641     | Carcass weight (kg)       | 346.72 | 53.15  | 15.41 |
|                         | Conformation <sup>1</sup> | 6.35   | 2.25   | 35.43 |
|                         | Fat <sup>2</sup>          | 6.67   | 1.85   | 27.73 |
|                         | Age at slaughter (days)   | 810.26 | 129.45 | 15.98 |
| Young bulls<br>n=86,089 | Carcass weight (kg)       | 368.71 | 64.84  | 17.58 |
|                         | Conformation <sup>1</sup> | 8.80   | 2.62   | 29.77 |
|                         | Fat <sup>2</sup>          | 5.27   | 0.99   | 18.77 |
|                         | Age at slaughter (days)   | 583.12 | 87.61  | 15.02 |

<sup>1</sup>Scored on a 15 point scale 1 (worst) to 15 (best).

<sup>2</sup>Scored on a 15 point scale 1 (lean) to 15 (fat).

n = number of animals in each gender.

### *Variance Components*

A quadratic random Legendre polynomial on sire fitted the data best for all traits and genders. A quadratic random Legendre polynomial on herd-year also fitted the data best for all traits and genders. Residual variances were heterogeneous across age (Appendix A). Young bulls had greater residual variation for all three traits, except for fat score, where the residual variance was greatest in heifers.

Genetic variances followed similar trends for all traits and genders, increasing as age at slaughter increased (Figure 2.3). The ranges of genetic variance estimates were similar across gender for carcass weight and conformation. Average genetic variance estimates were greatest for fat score in steers ( $0.57 \pm 0.04$  units<sup>2</sup>) whereas the least genetic variation for fat score was observed among young bulls ( $0.16 \pm 0.02$  units<sup>2</sup>).

Heritability estimates for carcass weight across ages of slaughter were greater in heifers ( $0.17 \pm 0.02$  to  $0.34 \pm 0.02$ ) and steers ( $0.21 \pm 0.01$  to  $0.27 \pm 0.01$ ) than in young bulls ( $0.08 \pm 0.02$  to  $0.16 \pm 0.01$ ). Peak heritability for carcass weight corresponded to the greatest estimates of genetic variation (Figure 2.4). Fat score was more heritable in heifers than in steers and young bulls, ranging from  $0.28 (\pm 0.02)$  at 530 days of age at slaughter to  $0.39 (\pm 0.02)$  at 880 days of age at slaughter. Heritability estimates for conformation across genders increased as age of slaughter increased (Figure 2.4). This increase was greatest in heifers, where heritability of conformation increased from  $0.24 (\pm 0.02)$  at 530 days of age at slaughter to  $0.42 (\pm 0.02)$  at 871 days of age at slaughter. On average, conformation across age at slaughter and genders was the most heritable trait  $0.36 (\pm 0.01)$ , whereas carcass weight across age at slaughter and genders was the least heritable trait  $0.23 (\pm 0.01)$ .

(a)



(b)



(c)



**Figure 2.3** Estimates of genetic variance for (a) carcass weight, (b) conformation, and (c) fat in heifers (— — —), steers (· · ·), and young bulls (—). Standard errors of genetic variance estimates ranged from 20.72 to 67.57 (kg<sup>2</sup>) for carcass weight, from 0.04 to 0.10 (units<sup>2</sup>) for conformation, and from 0.01 to 0.09 (units<sup>2</sup>) for fat. Carcass conformation and fat scores were measured on a scale of 1 to 15.



(a)



(b)



(c)



**Figure 2.4** Heritability estimate for (a) carcass weight, (b) conformation, and (c) fat in heifers (— — —), steers (· · ·), and young bulls (—); standard errors of heritability estimates ranged from 0.01 to 0.02 for carcass weight, from 0.01 to 0.03 for conformation, and from 0.01 to 0.03 for fat.

The largest eigenvalues explained 81%, 90% and 95% of the genetic variation for carcass weight in heifers, steers and young bulls, respectively. In all the models, the largest proportion of the genetic variation was explained by the intercept term of the RRM. The eigenfunctions associated with the largest eigenvalues for carcass weight, conformation and fat were of the same sign across ages of slaughter in all genders (Figure 2.5). Similar to carcass weight, the intercept term explained the majority of the genetic variance for conformation (82%, 96% and 93% for heifers, steers and young bulls, respectively) and fat score (91%, 89% and 95% for heifers, steers and young bulls, respectively). Eigenfunction estimates relating to the second largest eigenvalues explained between 4% (conformation in steers) and 18% (carcass weight in heifers) of the genetic variability. The eigenfunctions corresponding to the second eigenvalues for carcass weight were the same sign across ages of slaughter in all genders except young bulls. The second eigenfunctions associated with conformation and fat were positive at early ages at slaughter and negative at older ages at slaughter in steers and young bulls (Figure 2.5).

(a)



(b)



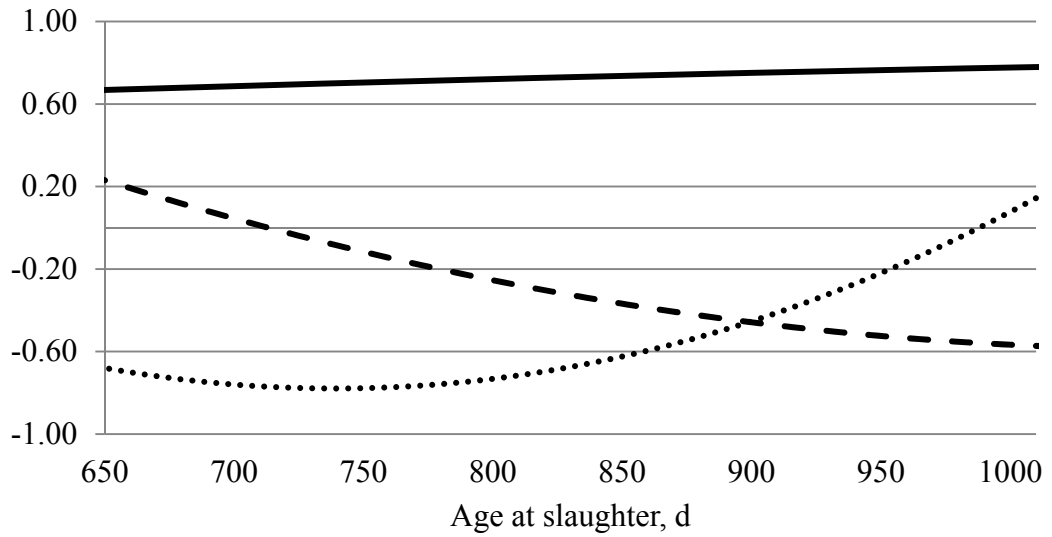
(c)



(d)

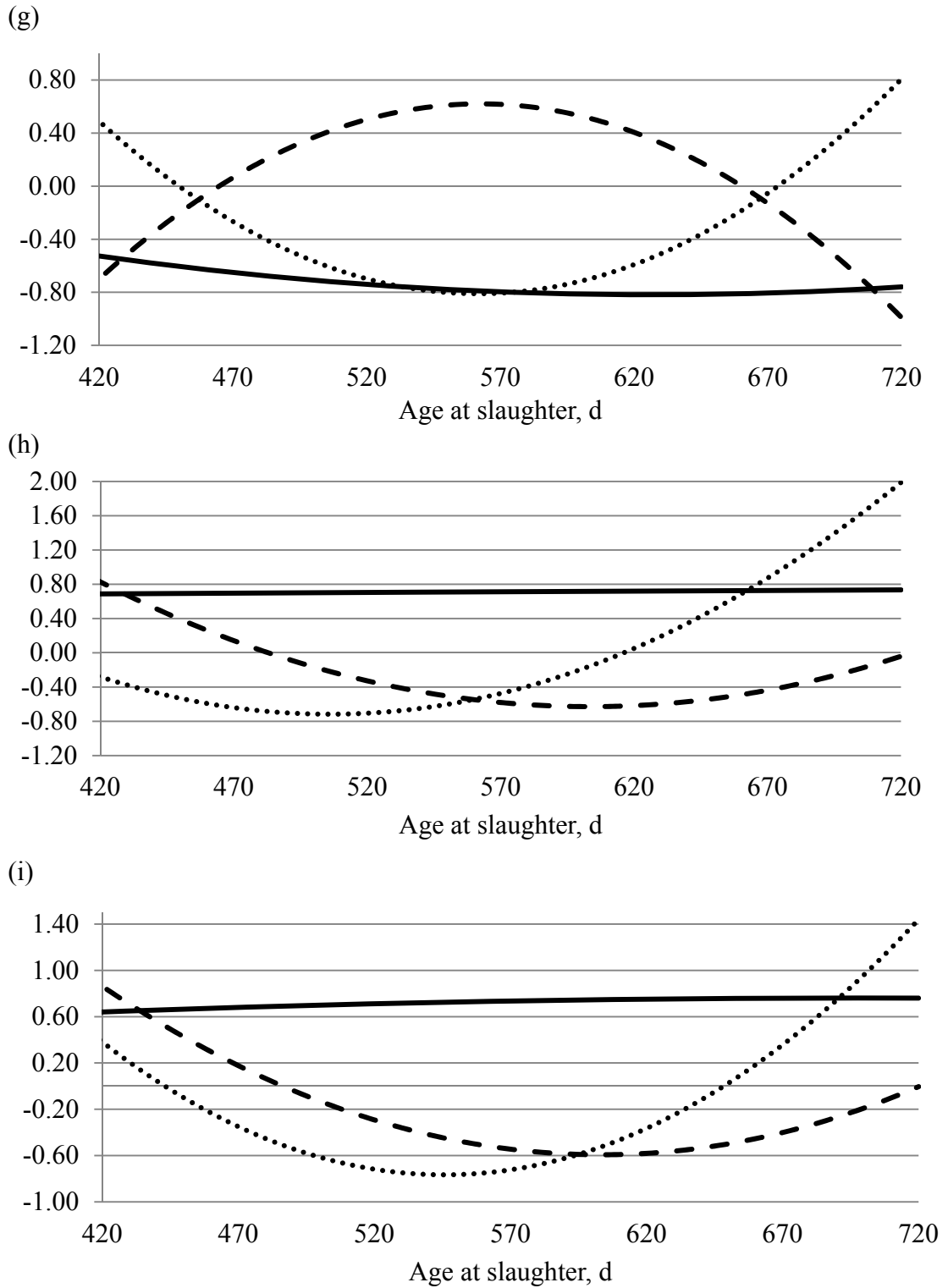


(e)



(f)





**Figure 2.5** Eigenfunctions (y-axis, unitless) associated with the largest (—), middle (— — —), and smallest (· · ·) eigenvalues in heifers for a) carcass weight, b) conformation, and c) fat and in steers, for d) carcass weight, e) conformation, and f) fat and in young bulls for g) carcass weight, h) conformation, and i) fat.

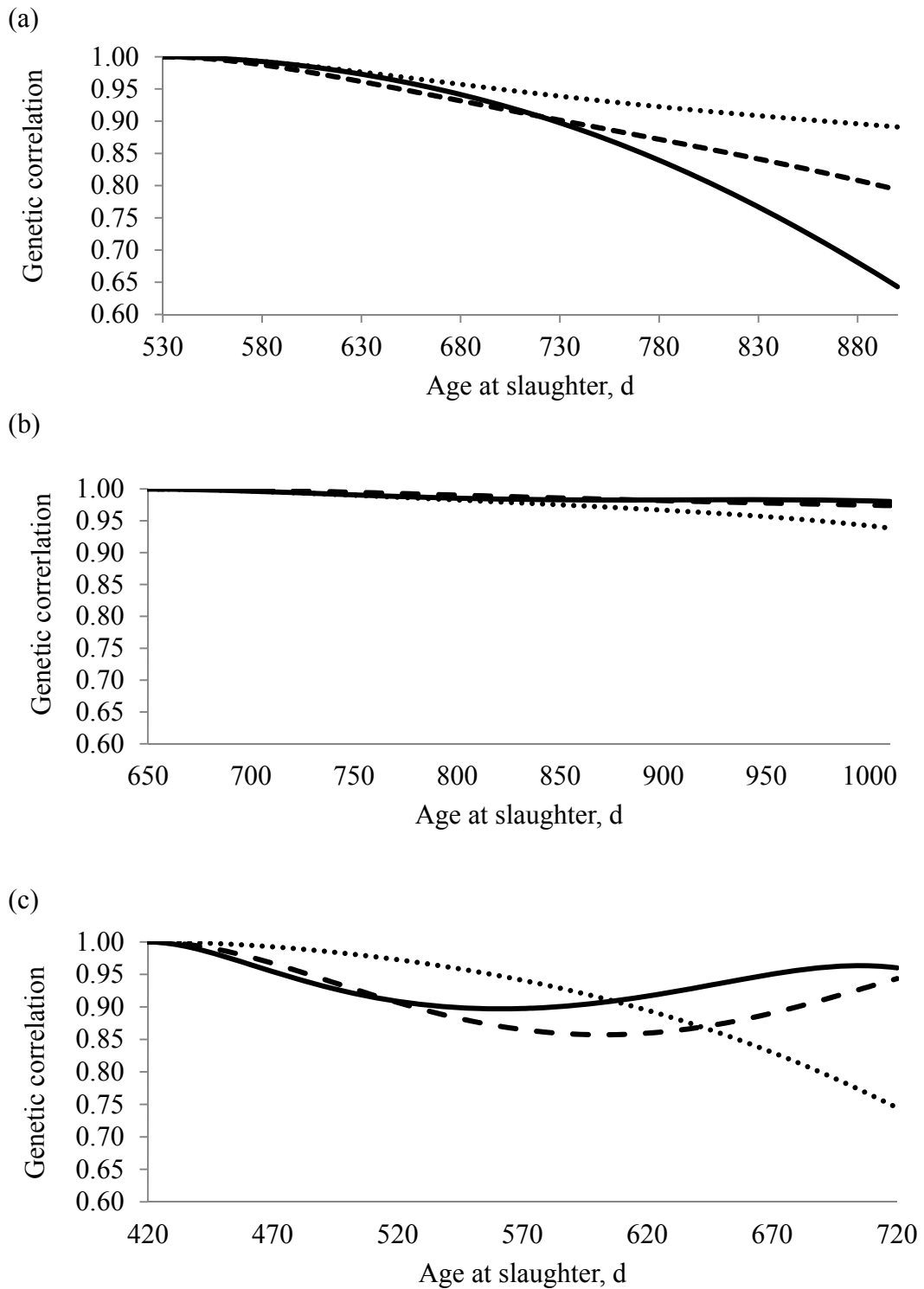
***Genetic correlations within trait***

Within trait genetic correlations across different ages at slaughter ranged from 0.64 ( $\pm 0.02$ ) to 1.00 ( $\pm 0.00$ ) in heifers, from 0.94 ( $\pm 0.01$ ) to 1.00 ( $\pm 0.00$ ) in steers, and from 0.74 ( $\pm 0.01$ ) to 1.00 ( $\pm 0.00$ ) in young bulls (Figure 2.6). Within trait correlations were strongest between adjacent ages, approaching unity, and weakened as the interval between ages lengthened. Across genders, within trait genetic correlations between youngest and oldest ages at slaughter were strongest for conformation scores and weakest for fat scores (Figure 2.6). The weakest genetic correlation 0.64 ( $\pm 0.02$ ) was observed in heifers between carcass weight at 530 days and 900 days of age at slaughter.

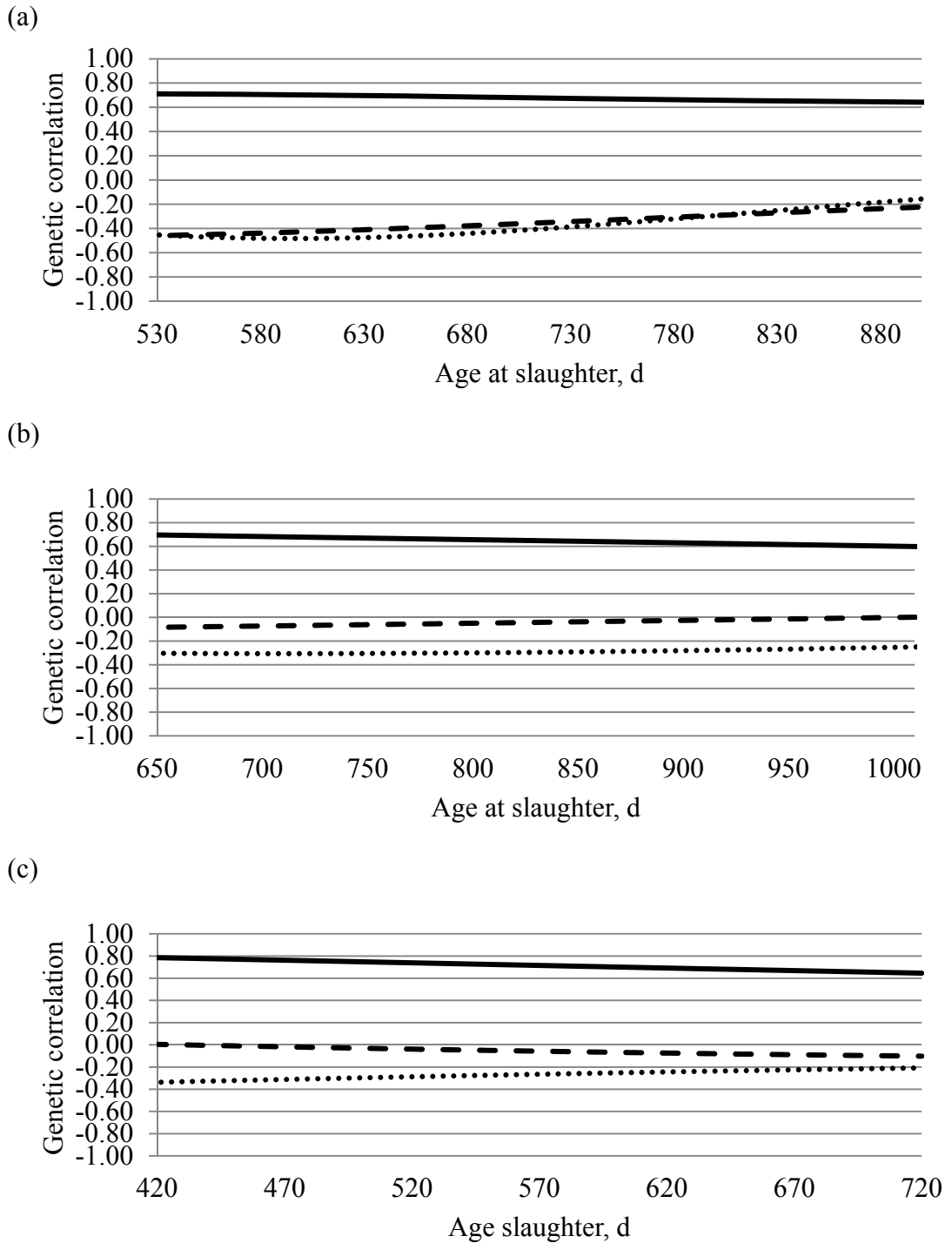
***Genetic correlations between traits***

Irrespective of gender, genetic correlations between carcass weight and conformation at the same age at slaughter were strongly positive reaching a maximum correlation of 0.78 ( $\pm 0.04$ ) in young bulls at 420 days of age at slaughter (Figure 2.7). In contrast, estimates of the genetic correlations between carcass conformation and fat score at the same age were negative. Genetic correlations between carcass weight and fat score were negative at younger slaughter ages and became weaker as age at slaughter increased. The weakest genetic correlation between carcass weight and fat was -0.48 ( $\pm 0.02$ ) at 597 days of age in heifers.

Strong positive to weak negative genetic correlations existed between carcass weight and the two other carcass traits, while the genetic relationship between fat and conformation varied around zero.



**Figure 2.6** Genetic correlations in a) heifers, b) steers, and c) young bulls between the first age and other ages at slaughter for carcass weight (—), conformation (— — —), and fat (· · ·); standard errors of genetic correlation estimates ranged from 0.00 to 0.02 for carcass weight, from 0.00 to 0.01 for conformation, and from 0.00 to 0.01 for fat.



**Figure 2.7** Genetic correlations across age for (a) heifers (b) steers, and (c) young bulls between carcass weight and conformation score (—), between conformation and fat score (— —), and between fat score and carcass weight (· · ·) across ages at slaughter. Standard errors of genetic correlation estimates ranged from 0.01 to 0.04 for carcass weight and conformation score, from 0.02 to 0.09 for conformation and fat score, and from 0.02 to 0.14 for carcass weight and fat score.



## **DISCUSSION**

### ***Modelling***

Growth curves that model both fixed and random effects are potentially a useful tool for selective breeding but also for precision-based management. Carcass development has mainly been modelled on a live weight basis using several different methods. These approaches include non-linear growth functions such as von Bertalanffy (von Bertalanffy, 1957), Gompertz (Winsor, 1932) and Brody (Brody, 1945), that describe the relationship between weight and age (Berry et al., 2005) using parameters with biological meaning. An additional approach includes multi-trait analyses considering different ages as separate traits (Nobre et al., 2003). Random regression models have previously been applied to growth studies where multiple live weight records exist (Meyer, 2001; Legarra et al., 2004). Studies that use RRM in the analysis of carcass growth are however, to our knowledge, non-existent. The present study used covariance functions to model growth rather than the traditionally used growth functions; an advantage of the former is that no prior assumptions about the shape of the curve over time are required (Meyer and Hill, 1997). In addition, modelling the covariance structure as a covariance function permits a gradual change in (co)variances at different ages at slaughter. A benefit of this was that it facilitated the estimation of covariance between ages for which no records necessarily existed (van der Werf et al., 1998) but also between different carcass characteristics at different ages.

The RRM fitted in the present study used Legendre polynomials, a function that is commonly used in the dairy industry to generate lactation profiles (Liu et al., 2003; Mrode et al., 2003). Legendre polynomials are favoured because their orthogonal

properties assist with model convergence (Brotherstone et al., 2000; Bohmanova et al., 2008); nonetheless, the fit may not be optimal at the extremes of the trajectory due to the scarcity of data at the extremities and the mathematical properties of polynomials (Legarra et al., 2004). The most parsimonious order of the polynomial term used, however, varies across studies. Nobre et al. (2003) used cubic Legendre polynomials to model growth curves in Nellore beef cattle, whereas, Arango et al. (2004) documented that the additive genetic covariance structure of live weight in beef cows could be described using linear random regression. The most parsimonious RRM in the present study was third order (i.e., quadratic) Legendre polynomials for the fixed and both random trajectories. Using equal orders of fixed and random effects have been suggested in the literature (Pool et al., 2000). Furthermore the analysis of eigenvalues of genetic covariance (Figure 2.5) for each trait, suggests the diminishing importance of adding further polynomial terms in explaining the additive genetic variance effects.

### ***Genetic parameters for carcass weight***

Carcass weight, which reflects lifetime growth, is a routinely evaluated trait in many beef genetic evaluations (Pabiou et al., 2011b). The genetic parameter estimates obtained in the present study using RRM corroborate those reported in other cattle populations estimated using traditional linear models (Gregory et al., 1995; Kause et al., 2015), including those from data on Irish cattle (Hickey et al., 2007; Pabiou et al., 2009; Pabiou et al., 2011a). The average heritability for carcass weight across genders and age at slaughter in the present study ( $0.23 \pm 0.01$ ) is similar to the estimate reported by Hickey et al. (2007) in Irish beef cattle, estimated using a linear animal model with a phenotypic adjustment for age. Hickey et al. (2007) reported varying direct

heritability estimates for carcass weight in cattle depending on breed composition, (0.17 for Aberdeen Angus or Belgian Blue sired to 0.65 Simmental sired).

Eigenfunctions are continuous functions whose coefficients are formed by the decomposition of the (co)variance matrices (Kirkpatrick and Heckman, 1989). Eigenfunctions provide information on how growth trajectories may change in response to selection (Meyer and Hill, 1997) and have previously been applied to live-weight records in dairy cows (Berry et al., 2003). Analysis of the eigenvalues and eigenfunctions of the additive genetic covariance matrices in the present study revealed genetic variability does indeed exist among animals in their growth profiles for carcass weight (Figure 2.5). Most of the genetic variance was however attributable to the intercept which suggests that the greatest opportunity exists to alter the height of growth profiles for carcass weight. This substantiates the strong positive genetic correlation that existed for carcass weight across different ages or in other words, selection for heavier carcass weights at any age would increase carcass weights at all ages (Figure 2.6). The strong genetic correlations between carcass weight at different ages corroborates documented genetic correlations from studies on live weight using both RRM (Arango et al., 2004) and traditional linear models (McHugh et al., 2014), where strong correlations existed between live weights at younger and older ages. The change in sign of the second eigenfunctions for carcass weight across ages in steers and young bulls, and in the third eigenfunctions in heifers and young bulls, provides evidence that exploitable genetic variation also exists in the shape of the growth curve (Figure 2.5). The genetic variation however was limited; therefore a greater weight would have to be imposed on the second and third eigenfunctions to alter the shape of the growth curves for carcass weight.

Generally in genetic evaluations of carcass traits, carcass weight at different ages is treated as the same trait (i.e., genetic correlation of unity among different ages) and age at slaughter adjustments are at the phenotypic level. The results in this present study mostly support this. Nonetheless, the existence of some moderate genetic correlations (i.e., as low as 0.64) between carcass weight in heifers between extreme ages suggests that, in fact carcass weight at extremely different ages in heifers may indeed be governed by different allelic variability. It has been proposed that genetic correlations of less than 0.80 may be different traits due to the existence of genotype-by-environment interactions and should therefore be treated as such (Robertson, 1959). Nonetheless, due to high computational requirements, the gain in accuracy of genetic evaluations may not justify the increased complexity of the genetic evaluation model that incorporates RRM.

#### ***Genetic parameters for carcass conformation and fat***

While RRM have previously been used to model animal (live-) weight in cattle (Meyer, 2000; Coffey et al, 2006), the use of RRM to model animal conformation or fat are non-existent in beef cattle although it has been undertaken in dairy cattle (Coffey et al, 2001). As with carcass weight, the heritability estimates for conformation and fat score were within the ranges of those reported from traditional linear models in other international beef populations (Rios-Utrera and Van Vleck, 2004) and in Irish populations (Hickey et al., 2007; Crowley et al., 2011; Pabiou et al., 2011a). Pabiou et al. (2011a), using data from Irish abattoirs, reported direct heritability estimates for conformation and fat score ranging from 0.28 to 0.46 and from 0.27 and 0.40, respectively from an animal linear mixed model. Similar to carcass weight, the constant positive eigenfunctions relating to the largest eigenvalues of

conformation and fat indicate an opportunity to alter the height of conformation and fat profiles to suit specific breeding objectives (Figure 2.5) and substantiates the strong genetic correlations that exist within each trait at different ages. The change in sign of the second and third eigenfunctions between younger and older ages at slaughter in steers and young bulls suggests the presence of factors with opposing effects on conformation and fat across ages at slaughter. Response to selection based on the second and third eigenvalues would be slow as they account for only less than 18% of the additive genetic variation; therefore, altering the shape of the profile through breeding may prove difficult as greater selection pressure would have to be imposed on the second and third eigenfunctions for conformation and fat.

***Genetic correlation between traits at the same age***

Estimates in the literature (Gregory et al., 1995; Kause et al., 2015) of the genetic correlations among carcass weight, conformation and fat vary widely among populations. Such variability may be due to differences in breeds or analytical methods used in the different studies. Based on results from the present study, these apparent discrepancies among studies may also be due to differently aged animals being included in the analysis. In the present study, increasing carcass weight was favourably related to better shaped carcasses in all genders. These strong positive correlations are consistent with those reported in the literature from traditional linear models (Van der Werf et al., 1998; Bouquet et al., 2010), but stronger than those reported from other Irish populations (Hickey et al., 2007; Pabiou et al., 2011a). Underlying genetic correlations influence the potential for change in carcass traits at different ages and will also impact the optimal age at which an animal should be slaughtered. In the present study, correlations between traits across age at slaughter and gender were

sufficiently different from unity, suggesting that heavier animals may also be more muscular and leaner at different ages at slaughter (Figure 2.7). The alleles affecting carcass weight and muscularity are different to those influencing fatness across ages at slaughter and therefore direct selection for heavier carcasses alone across all ages at slaughter does not necessarily have to result in fatter carcasses. Random regression analyses provide genetic information for carcass traits across all ages at slaughter and have the potential to be used in routine genetic analysis of carcass traits. Based on the genetic correlation structure between carcass traits across the trajectory, different emphasis may be placed in an index using information from different ages to facilitate optimal selection for combinations of carcass weight, conformation and fat levels at specific ages.

### ***Implications***

This study shows the genetic relationships among carcass traits across varying ages at slaughter in a population of Irish beef cattle using RRM. Results illustrate the potential to select on carcass trait trajectories and to alter growth curves to meet specific breeding objectives. Knowledge of the variability in genetic potential for carcass growth and both muscle and fat deposition is important in order to achieve genetic gain. Such information may also be useful in management decision support tools to align the management of animals more closely with their growth potential. For example, in a feedlot production system, grouping animals based on individual genetic growth profiles, as opposed to breed, may facilitate better management of resources. In addition, such grouping may aid in decisions on when best to slaughter pens of animal.

### **2.3 Chapter conclusion**

This chapter demonstrates that the application of random regression models to carcass trait evaluations is feasible. The implementation of random regression techniques to carcass trait evaluations provides information on the variability of carcass traits across all possible ages at slaughter. A large proportion of carcass performance at any slaughter age is related to the genetics of the animal. Results provide helpful information for beef breeders to improve selection strategies, such as identifying the optimum age at which to slaughter the progeny of sires based on individual sire genetic growth profiles.

## **Chapter 3: Herd-specific random regression carcass profiles for beef cattle after adjustment for animal genetic merit**



### **3.1 Chapter introduction**

The previous chapter explored an alternative methodology for the purpose of genetic evaluations of carcass data using random regression models across a time trajectory defined by the slaughter age of the progeny of the evaluated sires. Results demonstrated how cattle breeders may enhance carcass trait performance by utilising improved genetic selection tools. Nonetheless, the overall carcass trait phenotype is influenced by both the genetics of the animal and the environment in which it is raised. Therefore, this chapter explores the possibility that carcass data used in routine genetic evaluations may also be exploited to assess the impact of the finishing herd and inform herd management decisions. Results address the second objective of this thesis. The body of the chapter has been published in Meat Science.

The student conducted all the work related to this chapter under guidance from her supervisors (manuscript co-authors).

## 3.2 Manuscript

### **Herd-specific random regression carcass profiles for beef cattle after adjustment for animal genetic merit**

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#### **ABSTRACT**

Abattoir data are an important source of information for the genetic evaluation of carcass traits, but also for on-farm management purposes. The present study aimed to quantify the contribution of herd environment to beef carcass characteristics (weight, conformation score and fat score) with particular emphasis on generating finishing herd-specific profiles for these traits across different ages at slaughter. Abattoir records from 46,115 heifers and 78,790 steers aged between 360 and 900 days, and from 22,971 young bulls aged between 360 and 720 days, were analysed. Finishing herd-year and animal genetic (co)variance components for each trait were estimated using random regression models. Across slaughter age and gender, the ratio of finishing herd-year to total phenotypic variance ranged from 0.31 to 0.72 for carcass weight, 0.21 to 0.57 for carcass conformation and 0.11 to 0.44 for carcass fat score. These

parameters indicate that the finishing herd environment is an important contributor to carcass trait variability and amenable to improvement with management practices.

**Keywords:** cattle, carcass traits, herd management, random regression

## INTRODUCTION

Routinely collected abattoir data is an important source of information for genetic evaluations of beef carcass traits in many countries including Ireland (Pabiou et al., 2009), France (Laloë et al., 2007) Sweden (Eriksson et al., 2003) and the UK (Moore et al., 2014). Best Linear Unbiased Prediction is traditionally used to estimate genetic evaluations adjusted for systematic management effects. Geneticists are mainly interested in the genetic evaluations themselves with the environmental effects usually being fitted to simply account for systematic variation. These systematic environmental effects could, however, be useful for management purposes in decision support tools (Caccamo et al., 2008).

Random regression is a useful technique for the study of trait profiles across a time trajectory (Olori et al., 1999) and is widely used in dairy cattle to model milk lactation profiles (Cobuci et al., 2005; Jamrozik et al., 1998). Measurements need not necessarily originate from the same animal but an underlying covariance structure, such as pedigree linkages, could connect individual animals measured over time. It is therefore possible to longitudinally model a trait for different sires exploiting information on the genetic relatedness among progeny slaughtered at different ages, thereby providing several effective measurements per sire across a time trajectory (Englishby et al., 2016; Jonest et al., 1999). In addition to producing genetic trait profiles for beef carcass traits (Englishby et al., 2016), random regression models may also be used to model herd-specific trait profiles after accounting for differences in

animal genetic merit (De Roos et al., 2004). These herd-specific trait profiles provide information on how animals within a herd perform compared to their respective performance under average management conditions (Caccamo et al., 2008). The inclusion of herd-specific regression curves was first proposed by Gengler et al. (2000) and has since been applied to test-day models for management purposes in dairy cattle (Bastin et al., 2009; Caccamo et al., 2010; Mayeres et al., 2004).

The objective of the present study was to quantify the contribution of finishing herd-year environment to the variability in carcass characteristics in beef cattle with particular emphasis on generating herd-specific profiles for carcass traits across age at slaughter. Genetic components were also considered in the statistical model to account for their effect on the studied carcass traits. Results will be useful in the development of management tools that provide information to producers on their herd performance over years.

## **MATERIALS AND METHODS**

All data used in the present study were obtained from the UK national beef carcass database.

### ***Data***

Carcass weight (kg), carcass conformation score (scale 1 to 15) and carcass fat score (scale 1 to 15) records from 2,964,387 beef cattle slaughtered between the years 2002 and 2014 were available. Carcass weight is measured on average two hours after slaughter following the removal of the head, legs, thoracic and abdominal organs, and internal fats and hide. Carcass classification (conformation and fat scores) is estimated using the European EUROP grid method, via visual inspection of the carcass by trained graders (Craigie et al., 2012). For the purposes of the present study, the resulting

EUROP classification grades were transformed into a 15-point numeric scale in line with national genetic evaluations for conformation and fat scores as described in Englishby et al. (2016).

Animals without a recorded sire or dam were discarded. Records were restricted to animals that moved herd no more than three times during their lifetime in order to reduce noise accruing from the effects of multiple herd environments. Cows (i.e., females that had at least one recorded calving date) and bulls >720 days of age at slaughter were not further considered. The remaining 1,050,832 records were restricted to prime slaughter heifers and steers (castrated) slaughtered between 360 and 900 days of age, and young bulls <720 days of age at slaughter. Further edits removed animal records more than four standard deviations from the within gender (heifer, steer, or young bull) population mean carcass weight and age at slaughter. Furthermore, dam parity was restricted to 1 to 10 and parity was subsequently categorised as 1, 2, 3, 4, and  $\geq 5$ . Only progeny from sires with at least 5 paternal half-sibs were retained in order to achieve sufficient genetic linkage among herds. Following these edits, 258,875 carcass records remained.

Two contemporary groups were generated: 1) abattoir by date of slaughter and 2) finishing herd-year of slaughter. Contemporary groups with less than five records were omitted. Following these final edits, 147,876 animals from 7,742 contemporary groups of finishing herd-year of slaughter remained. Of these data, 46,115 were heifers, 78,790 were steers and 22,971 were young bulls. Animals included in the analysis were progeny of 8,817 sires.

### ***Data analysis***

Carcass weight, conformation score and fat score were analysed within gender using the following random regression model:

$$\begin{aligned}
 Y_{dhjklqnz} = & \mu + Parity_d + Abattoir\_DoS_h \\
 & + Dambreed_j + Sirebreed_k + a_1.Het + a_2.Rec + \\
 & \sum_{i=1}^n b_n P_n Age + \sum_{i=1}^n HY_{ln} P_n Age + \\
 & \sum_{i=1}^n Sire_{qn} P_n Age + e_{dhjklqnz}
 \end{aligned}
 \tag{3.1}$$

Where  $Y_{dhjklqnz}$  = the observed record for carcass weight, carcass conformation score or carcass fatness score on animal  $z$ ;  $\mu$  = the population mean;  $Parity_d$  = fixed effect of the  $d^{th}$  parity of the dam of animal  $z$  (5 levels);  $Abattoir\_DoS_h$  = fixed effect of abattoir by date of slaughter interaction  $h$  (9,154 levels);  $Dambreed_j$  = fixed effect of breed  $j$  of dam of animal  $z$  (56 levels);  $Sirebreed_k$  = fixed effect of breed  $k$  of sire of animal  $z$  (52 levels);  $a_1$  = linear regression coefficient on heterosis (Het) in animal  $z$ ;  $a_2$  = linear regression coefficient on recombination loss (Rec) in animal  $z$ ;  $b_n$  = fixed regression coefficient on age at slaughter (Age) modelled with  $n^{th}$  order Legendre polynomial (Pn);  $HY_{ln}$  = random regression coefficient on age at slaughter associated with the effect of finishing herd-year  $l$ , representing management practices;  $Sire_{qn}$  = random regression coefficient on age at slaughter associated with the genetic effect of sire  $q$  of animal  $z$ , including all available pedigree data (42,773 additional non-founder animals);  $e_{dhjklqnz}$  = residual error term for age class.

Coefficients of heterosis and recombination loss were calculated for each animal as follows (Van der Werf and de Boer, 1989):

$$\text{Heterosis (Het)} = P_S (1 - P_D) + P_D (1 - P_S)$$

$$\text{Recombination (Rec)} = P_D (1 - P_D) + P_S (1 - P_S)$$

Where  $P_S$  and  $P_D$  = the proportions of the primary genetic group in the sire and the dam, respectively. The genetic groups were formed by the compression of 56 breed types into 4 genetic groups based on pedigree information and the assumption of some common ancestry among the breeds of each genetic group (continental beef breeds, dual purpose breeds, native UK breeds, and all other breeds). As there were 4 genetic groups defined this resulted in 6 heterosis and 6 recombination loss terms which were summed to produce an overall heterosis value and an overall recombination loss value for each animal.

Residual errors across age at slaughter were expected to have heterogeneous variances, possibly due to different management practices; therefore, different residual error classes associated with different ages at slaughter were modelled. The data of heifers and steers was divided into 12 classes and the young bull data into 8 classes as described in Table 3.1. Within class, residual variances were assumed to be homogenous and co-variances between classes were assumed to be zero.

**Table 3.1** Numbers of heifer, steer, and young bull records per residual variance class representing age at slaughter.

| Class (days) | Heifers | Steers | Young Bulls |
|--------------|---------|--------|-------------|
| 360-405      | 133     | 386    | 3,680       |

|         |       |        |       |
|---------|-------|--------|-------|
| 406-450 | 574   | 1,228  | 7,459 |
| 451-495 | 1,245 | 1,874  | 8,632 |
| 496-540 | 2,441 | 3,416  | 1,843 |
| 541-585 | 4,616 | 6,569  | 793   |
| 586-630 | 7,193 | 9,409  | 328   |
| 631-675 | 7,491 | 11,923 | 166   |
| 676-720 | 6,900 | 12,477 | 70    |
| 721-765 | 5,405 | 10,506 | N/A   |
| 766-810 | 4,288 | 8,676  | N/A   |
| 811-855 | 3,386 | 6,850  | N/A   |
| 856-900 | 2,443 | 5,526  | N/A   |

N/A= not applicable

In model (3.1), the fixed regression coefficient on age at slaughter was associated with an overall curve for each trait and gender, whereas the random regressions modelled both individual finishing herd-year contemporary group deviations and individual animal deviations from the overall curve.

Univariate and bivariate analyses based on model (3.1) were used to estimate variance and covariance components for each of the carcass traits. For the bivariate analyses, the same fixed and random effects were fitted for all traits. Different orders of Legendre polynomials were tested. Model building and the goodness of fit was determined as described by Englishby et al. (2016). All analyses were conducted using the AsReml software (Gilmour et al., 2009)

#### *(Co)variance components*

Finishing herd-year and genetic (co)variance function coefficients for each trait were fitted using the model suggested by Kirkpatrick & Heckman (1989):

$$G = \Phi'K\Phi$$

Where  $G$  is the (co)variance matrix for slaughter ages,  $\Phi$  is the matrix of Legendre polynomial age regression coefficients, and  $K$  is the estimated (co)variance matrix of the random polynomial coefficients (finishing herd-year or sire; in the latter case,



variance was multiplied by four to convert to a genetic variance estimate (Huisman et al., 2002). Model solutions for the random effects were used to derive two sets of curve coefficients, one per finishing herd-year and one per sire, facilitating estimates and inference to be made about environmental and genetic effects, respectively, across the trajectory.

The estimates of (co)variance components were used to calculate variance ratios for each trait at different ages at slaughter as well as correlations between finishing herd-year effects and between carcass traits at different ages at slaughter. Approximate standard errors of the variance ratios were derived using a Taylor series expansion (Fischer et al., 2004); approximate standard errors of correlations were calculated using the methodology described in Falconer and MacKay (1996). Eigenvalues and eigenfunctions of the finishing herd-year and genetic (co)variance matrices of polynomial coefficients were calculated to determine their overall contribution to the trait curves.

## **RESULTS**

Phenotypic statistics for carcass weight, conformation and fat scores in each gender are in Table 3.2. Heifers were slaughtered at an average age of 676 days and were the fattest of the three genders. Young bulls had the heaviest mean carcass weight, highest conformation score and lowest fat score of the three genders.

There were 1,582 finishing herds containing heifers, 1,278 finishing herds containing steers, and 525 finishing herds containing young bulls, and each with an average of 43, 59 and 44 animals, respectively. An average of approximately 4 sires was used per herd.

The fixed regression trajectories were best modelled as cubic regressions in all instances. Third order Legendre polynomials had the best parsimony to account for random finishing herd-year and sire variances across all traits and genders except for sire variances in young bulls which was best modelled with a second order Legendre polynomial.

#### ***Finishing herd-year parameters***

The pattern of the ratio of finishing herd-year variance to total phenotypic variance across different ages at slaughter is presented in Figure 3.1. Average estimates across all ages at slaughter are shown in Table 3.2, along with corresponding trait average heritability estimates for comparison. All estimates of finishing herd-year variance to total phenotypic variance ratios and estimates of heritability (genetic to phenotypic variance ratios) were greater ( $P < 0.05$ ) than zero. Estimates of finishing herd-year variance to total phenotypic variance and estimates of heritability for ages at slaughter between 360 to 405 days in heifers and steers, and those for ages between 631 to 720 days in young bulls, were not reported due to the low numbers of records and large associated standard errors in these age groupings. Across gender, finishing herd-year variance for carcass weight accounted for between 30.83% and 71.48% of the total phenotypic variation (Figure 3.1). Finishing herd-year variance estimates for conformation score (Figure 3.1) accounted for less phenotypic variation across age at slaughter in young bulls (21.68%-26.29%) than in heifers (25.06%-32.51%) or steers (30.83%-56.22%). The lowest finishing herd-year variance ratios were observed for fat score (Figure 3.1) across gender explaining between 10.88% (fat at 628 days of age at slaughter in young bulls) and 44.04% (fat at 405 days of age at slaughter in heifers) of the total phenotypic variance. As young bulls aged, the influence of herd

management on carcass weight and conformation score remained constant, whereas the influence of management on fat score decreased. In steers and heifers, management effects across age at slaughter decreased as animals aged for all carcass traits except for the influence of management on conformation score in heifers which remained constant across age at slaughter.

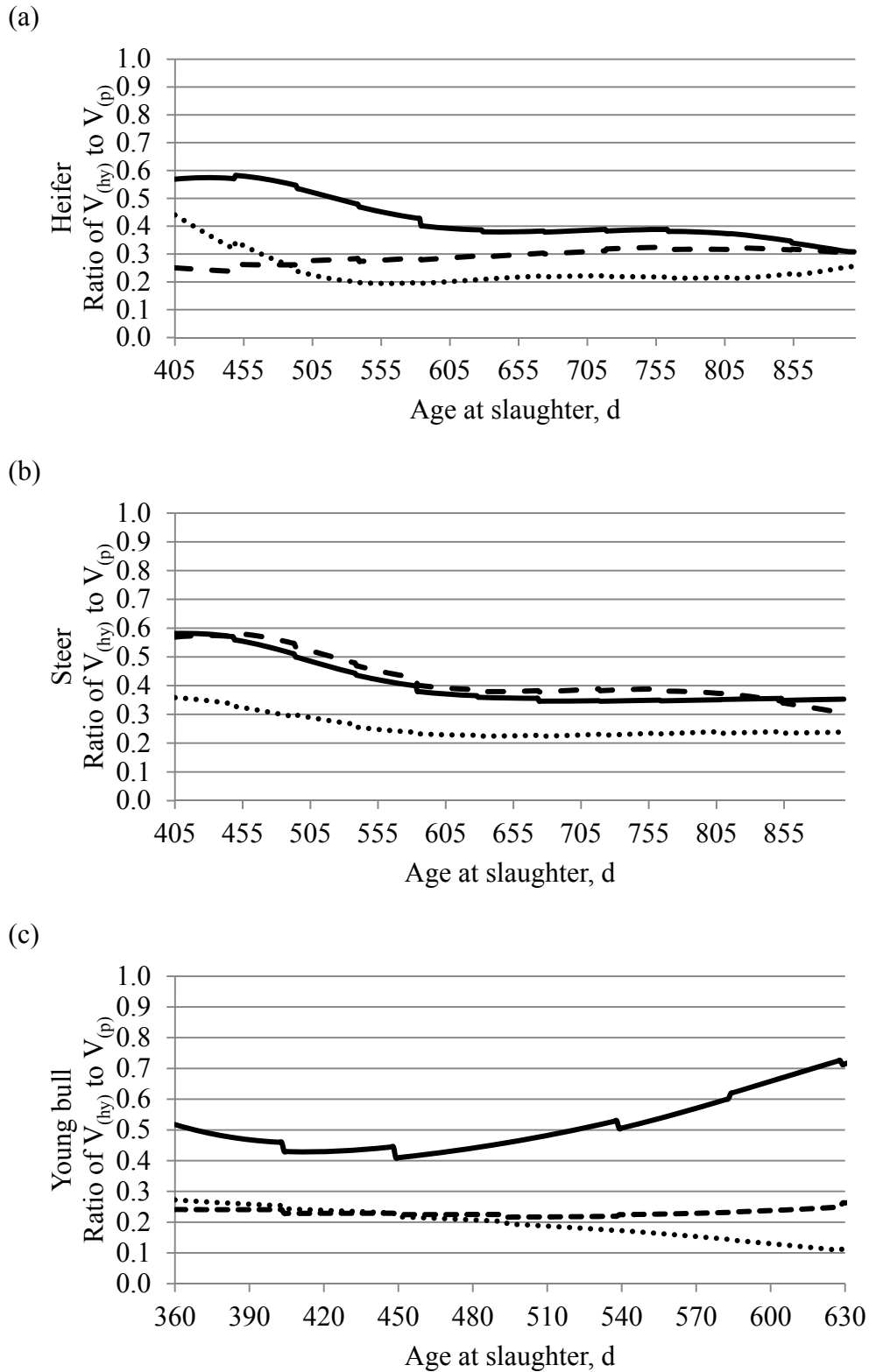
Eigenvalues and eigenfunctions derived from the finishing herd-year (co)variance matrices are shown in Table 3.3 and Figure 3.2 (steers only), respectively. Each eigenvalue was expressed as a percentage of the sum of all eigenvalues to determine its relative importance. The largest proportion of the variance in finishing herd-year was explained by the first eigenvalue, which ranged from 48.63% for fat score in heifers to 93.30% for fat score in young bulls. The largest eigenvalue corresponded to the intercept term in all models, which represents the height of the finishing herd-year profiles for each carcass trait. The second and third eigenvalues combined, which represent the shape of the finishing herd-year profiles accounted for between 6.70% (fat score in young bulls) and 51.37% (fat score in heifers) of the variation in carcass traits across ages at slaughter.

**Table 3.2** Mean, standard deviation (sd), coefficient of variation (CV%), average heritability ( $h^2$ ) estimates ( $\pm$ SE) and average ratio of finishing herd-year of slaughter to phenotypic variance estimates ( $\pm$ SE) for each gender by carcass trait.

| Gender                  | Trait                     | Mean   | s.d    | CV%   | $h^2$             | $V_{hy}/V_p$      |
|-------------------------|---------------------------|--------|--------|-------|-------------------|-------------------|
| Heifers<br>n=46,115     | Carcass weight (kg)       | 292.72 | 35.53  | 12.14 | 0.30 $\pm$ (0.02) | 0.43 $\pm$ (0.02) |
|                         | Conformation <sup>1</sup> | 7.32   | 1.51   | 20.63 | 0.34 $\pm$ (0.02) | 0.29 $\pm$ (0.03) |
|                         | Fat <sup>2</sup>          | 10.26  | 1.55   | 15.11 | 0.39 $\pm$ (0.03) | 0.24 $\pm$ (0.02) |
|                         | Age at slaughter (d)      | 676.23 | 105.47 | 15.59 |                   |                   |
| Steers<br>n=78,790      | Carcass weight (kg)       | 334.06 | 41.49  | 12.42 | 0.34 $\pm$ (0.02) | 0.41 $\pm$ (0.02) |
|                         | Conformation <sup>1</sup> | 7.44   | 1.48   | 19.84 | 0.38 $\pm$ (0.02) | 0.43 $\pm$ (0.02) |
|                         | Fat <sup>2</sup>          | 9.84   | 1.49   | 15.02 | 0.38 $\pm$ (0.02) | 0.26 $\pm$ (0.02) |
|                         | Age at slaughter (d)      | 690.69 | 108.65 | 23.82 |                   |                   |
| Young bulls<br>n=22,971 | Carcass weight (kg)       | 354.27 | 52.18  | 14.72 | 0.23 $\pm$ (0.03) | 0.40 $\pm$ (0.04) |
|                         | Conformation <sup>1</sup> | 9.31   | 2.16   | 23.20 | 0.50 $\pm$ (0.03) | 0.23 $\pm$ (0.03) |
|                         | Fat <sup>2</sup>          | 8.18   | 2.02   | 24.69 | 0.47 $\pm$ (0.03) | 0.16 $\pm$ (0.03) |
|                         | Age at slaughter (d)      | 454.77 | 51.35  | 11.29 |                   |                   |

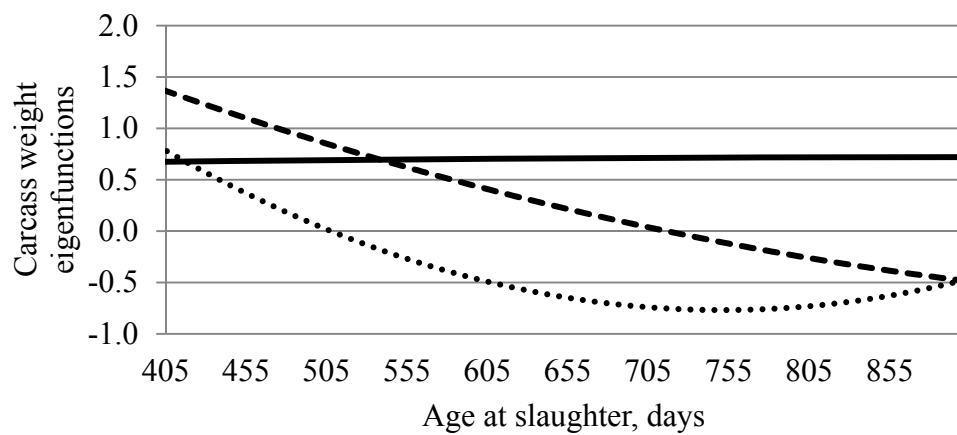
<sup>1</sup>Scored on a 15 point scale 1 (worst) to 15 (best).<sup>2</sup>Scored on a 15 point scale 1 (leanest) to 15 (fattest).

n = number of animals.

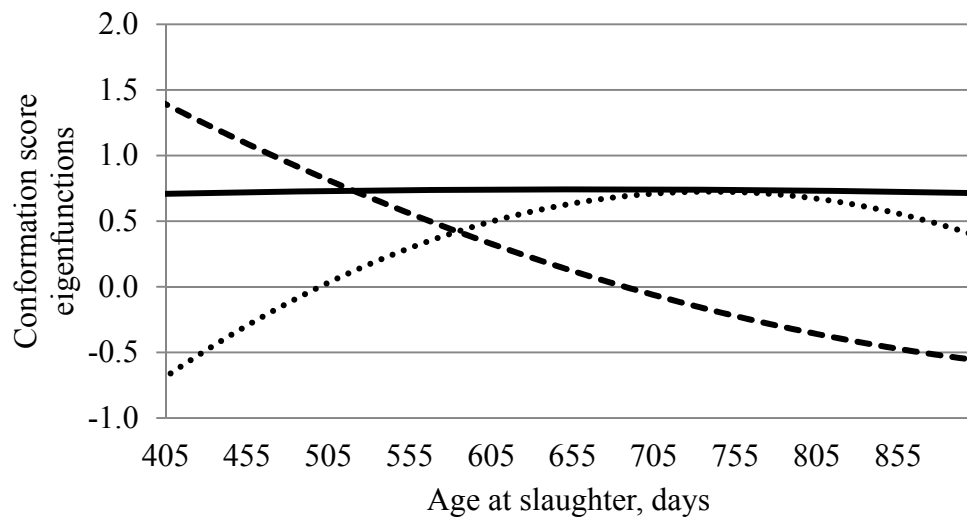


**Figure 3.1** Ratio of finishing herd-year variance to total phenotypic variance in (a) heifers, (b) steers and (c) young bulls, for carcass weight (—), conformation (— — —) and fat (· · ·); standard errors ranged from 0.02 to 0.10 for carcass weight, 0.01 to 0.10 for conformation score and 0.2 to 0.11 for fat score.

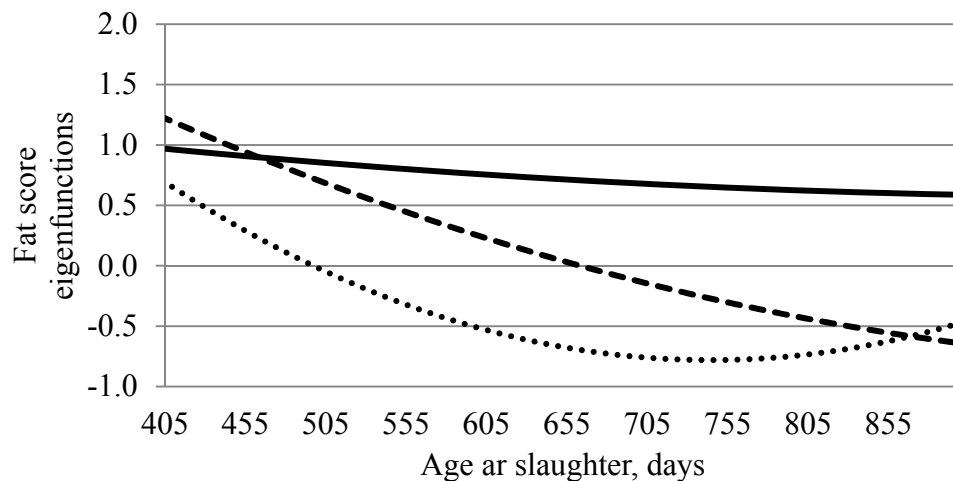
(a)



(b)



(c)



**Figure 3.2** Eigen functions associated with the first (—), second (---) and third (···) eigenvalues of finishing herd-year variance in steers for (a) carcass weight, (b) conformation score and (c) fat score.

**Table 3.3** Eigenvalues and their proportions for the herd-year of slaughter variance covariance matrices for carcass traits in each gender.

| Gender      | Trait          | Eigenvalue% |        |       |
|-------------|----------------|-------------|--------|-------|
|             |                | First       | second | third |
| Heifers     | Carcass weight | 57.80       | 37.15  | 5.05  |
|             | Conformation   | 72.32       | 21.85  | 5.83  |
|             | Fat            | 48.63       | 38.25  | 13.12 |
| Steers      | Carcass weight | 57.53       | 34.82  | 7.55  |
|             | Conformation   | 64.56       | 29.40  | 6.04  |
|             | Fat            | 62.58       | 30.06  | 7.36  |
| Young bulls | Carcass weight | 82.67       | 14.73  | 2.60  |
|             | Conformation   | 85.00       | 14.50  | 0.50  |
|             | Fat            | 93.30       | 5.88   | 0.82  |

In steers, the direction of the largest eigenfunction associated with the leading eigenvalues was constant across ages at slaughter, whereas the sign changes across age at slaughter were associated with the eigenfunctions of the second and third eigenvalues for all traits (Figure 3.2). Similar trends in the direction of eigenfunctions existed for all carcass traits in young bulls and heifers (results not shown) with the exception of fat score in heifers where the direction of the largest eigenfunction changed from negative to positive as age at slaughter increased.

#### ***Finishing herd-year correlations within trait***

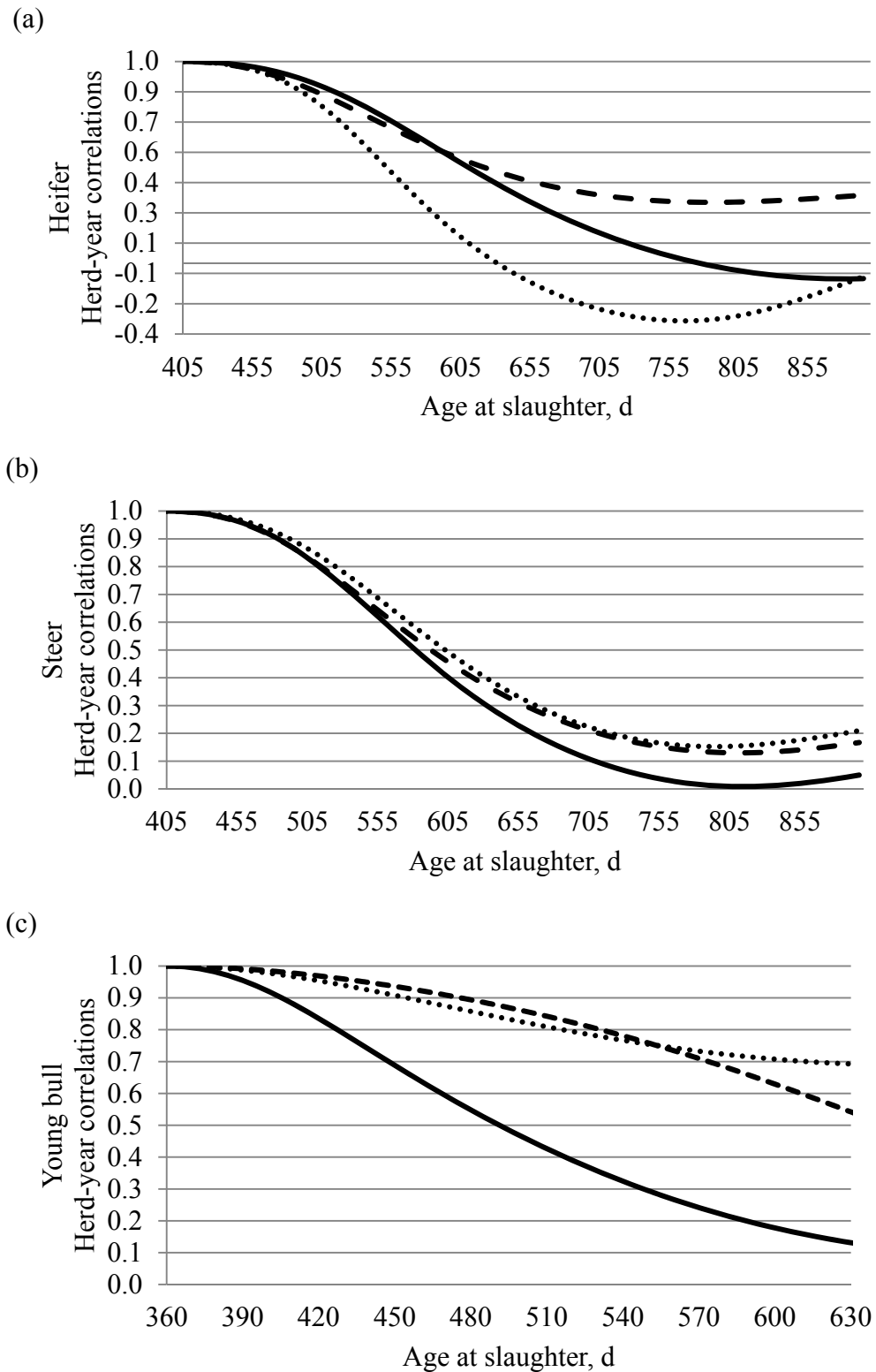
Correlations between the herd-year effects in the youngest and all subsequent ages at slaughter varied from -0.28 ( $\pm 0.03$ ) to 1.00 ( $\pm 0.00$ ) in heifers, from 0.01 ( $\pm 0.03$ ) to 1.00 ( $\pm 0.00$ ) in steers, and from 0.13 ( $\pm 0.05$ ) to 1.00 ( $\pm 0.00$ ) in young bulls (Figure 3.3). Within trait correlations weakened with increasing interval between ages at slaughter. Irrespective of gender, finishing herd-year correlations between youngest and oldest ages at slaughter were strongest for conformation score. Negative

correlations between herd-years effects were observed in heifers between fat score at 405 days and all ages at slaughter beyond 632 days, and between carcass weights at 405 days and all slaughter ages beyond 777 days (Figure 3.3).

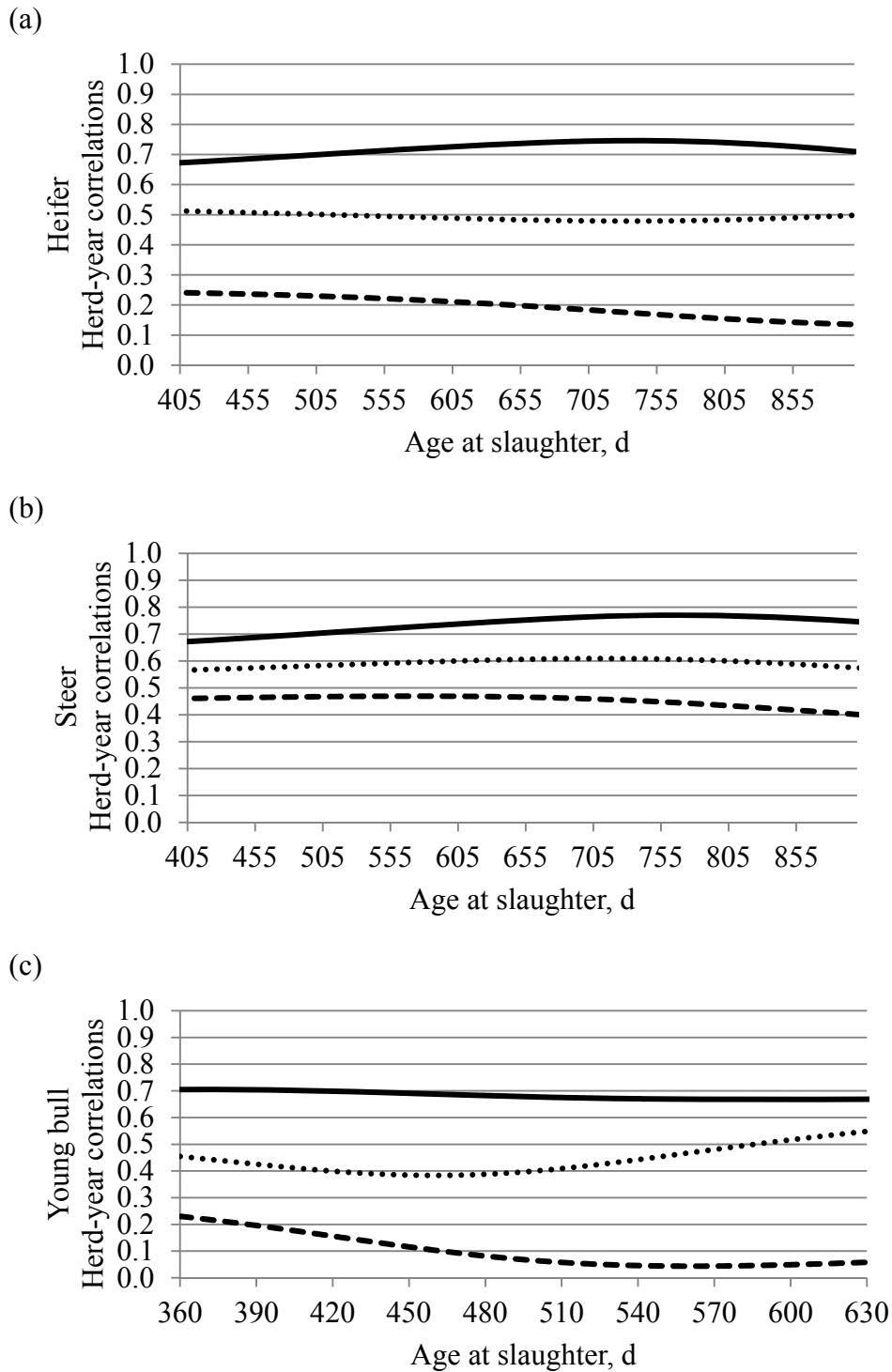
***Correlations between herd-year effects on different carcass traits***

The strongest correlations between traits at the same age at slaughter were between carcass weight and conformation score in all genders, ranging from 0.67 ( $\pm 0.04$ ) at 594 days in young bulls to 0.77 ( $\pm 0.01$ ) at 769 days in steers (Figure 3.4). Regardless of gender, positive correlations also existed between carcass weight and fat score across age at slaughter. The weakest correlations across age at slaughter occurred between conformation and fat score in all genders. A practically zero correlation of 0.04 ( $\pm 0.12$ ) existed between these two traits at 561 days of age at slaughter in young bulls.





**Figure 3.3** Finishing herd-year correlations between the earliest and all subsequent ages at slaughter in (a) heifers, (b) steers and (c) young bulls, for carcass weight (—), conformation score (— — —) and fat score (· · ·); standard errors ranged from 0.00 to 0.07 for carcass weight, 0.00 to 0.11 for conformation score and 0.00 to 0.18 for fat score.

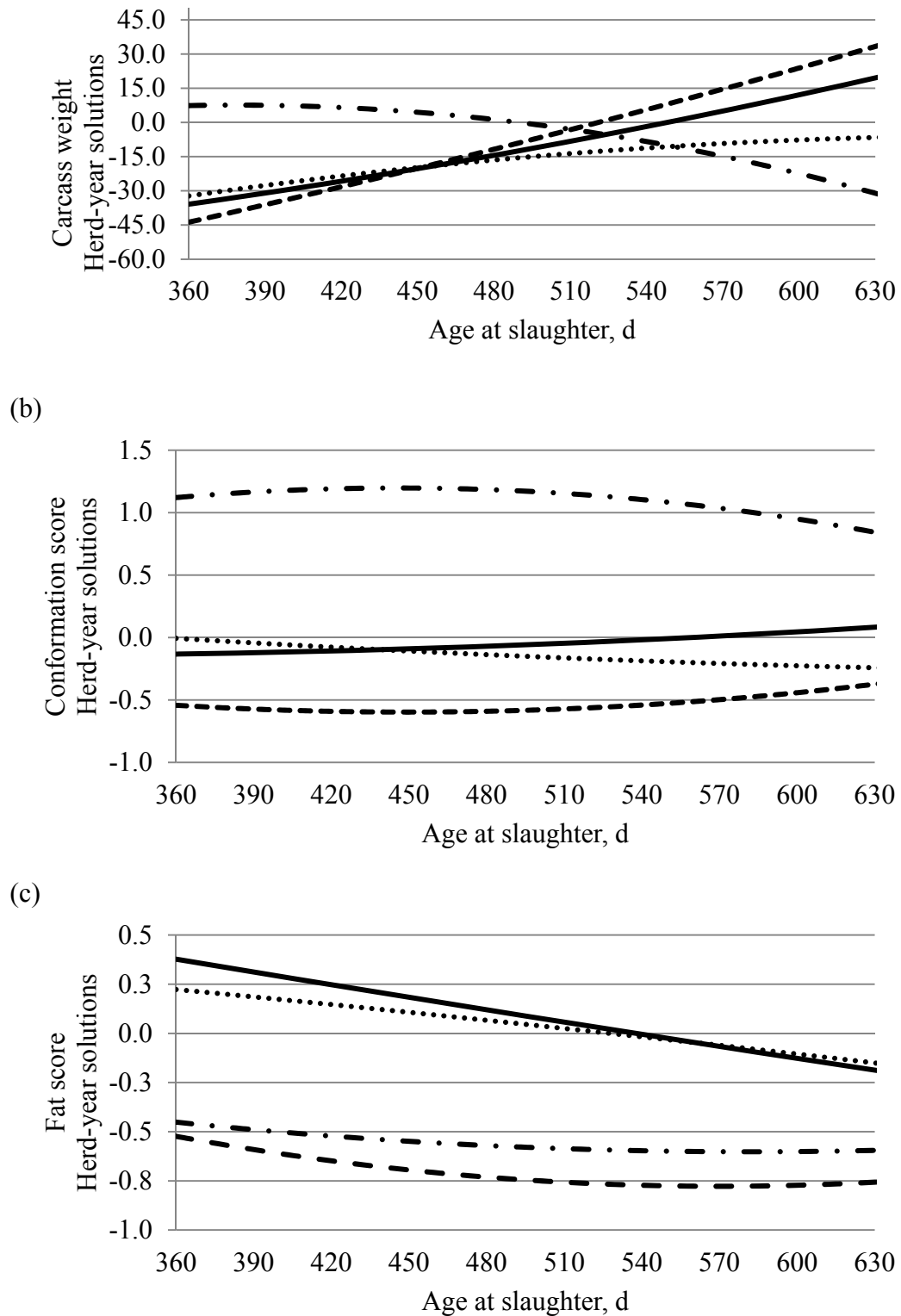


**Figure 3.4** Finishing herd-year correlations between carcass weight and conformation score (—), conformation score and fat score (---), and carcass weight and fat score (···) across ages at slaughter for (a) heifers, (b) steers and (c) young bulls; standard errors ranged from 0.01 to 0.06 between carcass weight and conformation score, 0.02 to 0.23 between conformation score and fat score, and 0.02 to 0.10 between carcass weight and fat score.

***Finishing herd-year curves for carcass traits***

The herd-year solution curves for young bulls slaughtered in three example finishing herds in the year 2011 relative to the mean (fixed) curve are shown in Figure 3.5. The management practices in herds A and B resulted in carcass weights that were similar to those of young bulls reared under average management conditions at younger age of slaughter (until 451 and 448 days, respectively) (Figure 3.5). Older bulls in herd A performed better than in the average herd whereas bulls in herd B had a below average performance when slaughtered at older ages. In contrast, herd C, had excellent management conditions for early slaughter ages but relatively poor performance at older ages at slaughter. For conformation, the management practices of herd C produced better shaped carcasses across all slaughter ages compared to the population average whereas the opposite was true for herd A (Figure 3.5). Herds A and C produced carcasses that were leaner compared to average management conditions across all slaughter ages, whereas herd B performed close to the average (Figure 3.5).

(a)

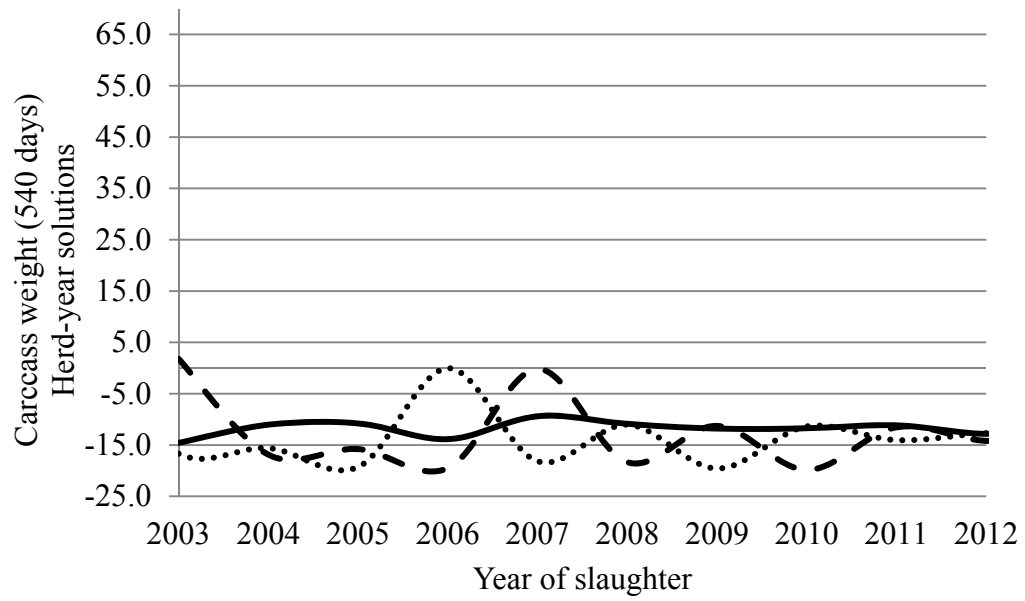


**Figure 3.5** Overall fixed finishing herd curves (—) for young bulls slaughtered in one year and three individual finishing herd curves, A (---), B (···) and C (—•—•), in the same year for (a) carcass weight, (b) conformation score and (c) fat score.

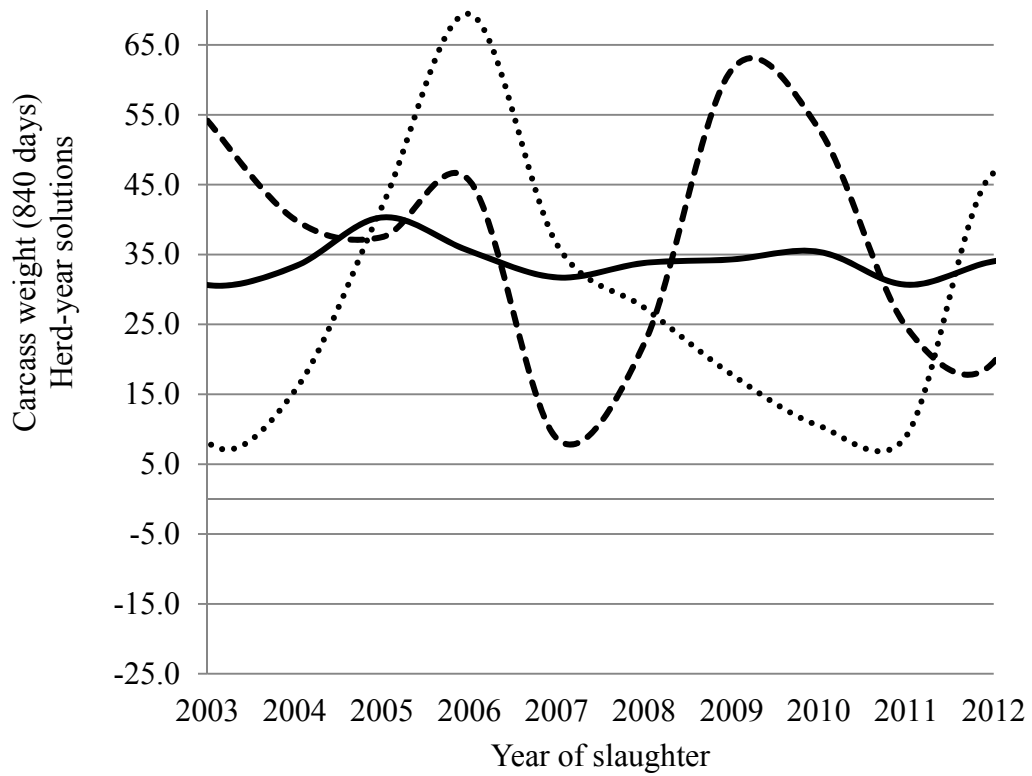
*Within finishing herd deviations across year of slaughter*

Clear variability in the influence of the herd management practices on carcass traits existed across year of slaughter. Figure 3.6 illustrates variability in herd management effects on carcass traits at two distinct slaughter ages (540 and 840 days), across year in two example herds of steers compared to the respective population average. The overall fixed curve demonstrates average management practices per age at slaughter across years whereas individual herd curves reflect management deviations from this average. The influence of management practices on carcass traits in these herds fluctuated greatly across year, in comparison to the average herd performance. The pattern of the management impact on carcass weight at the early slaughter age was not necessarily reflective of changes at older ages at slaughter (Figure 3.6). In general, similar trends were observed between carcass conformation and fat score (Figure 3.6) across the year of slaughter trajectory. The corresponding patterns in the two other genders (heifers and young bulls) were similar (results not shown).

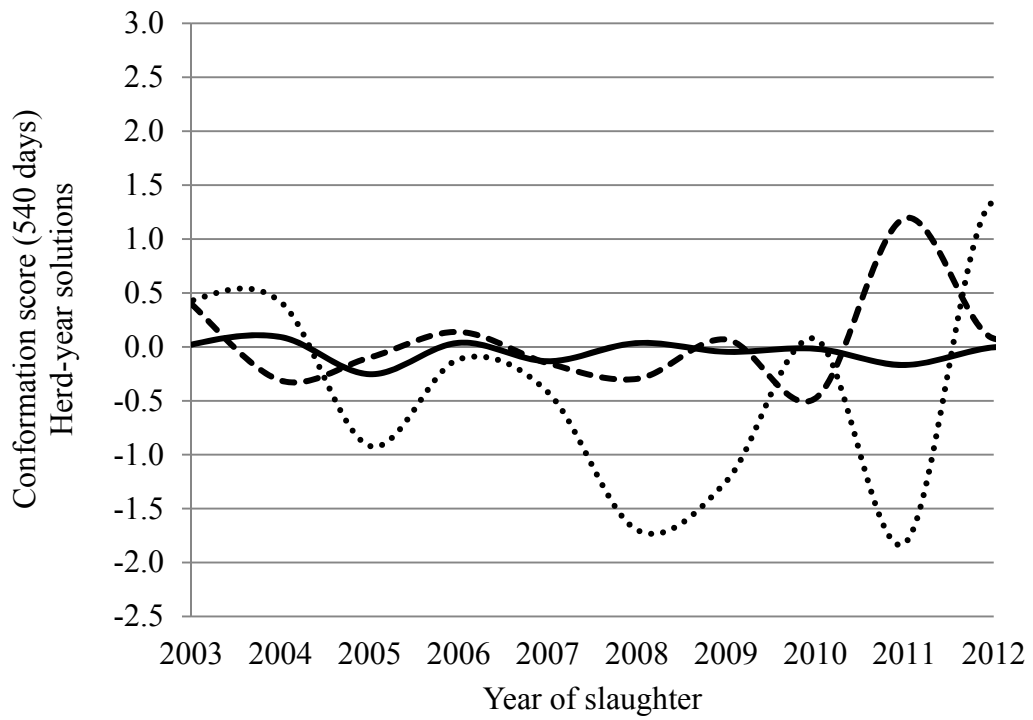
(a)



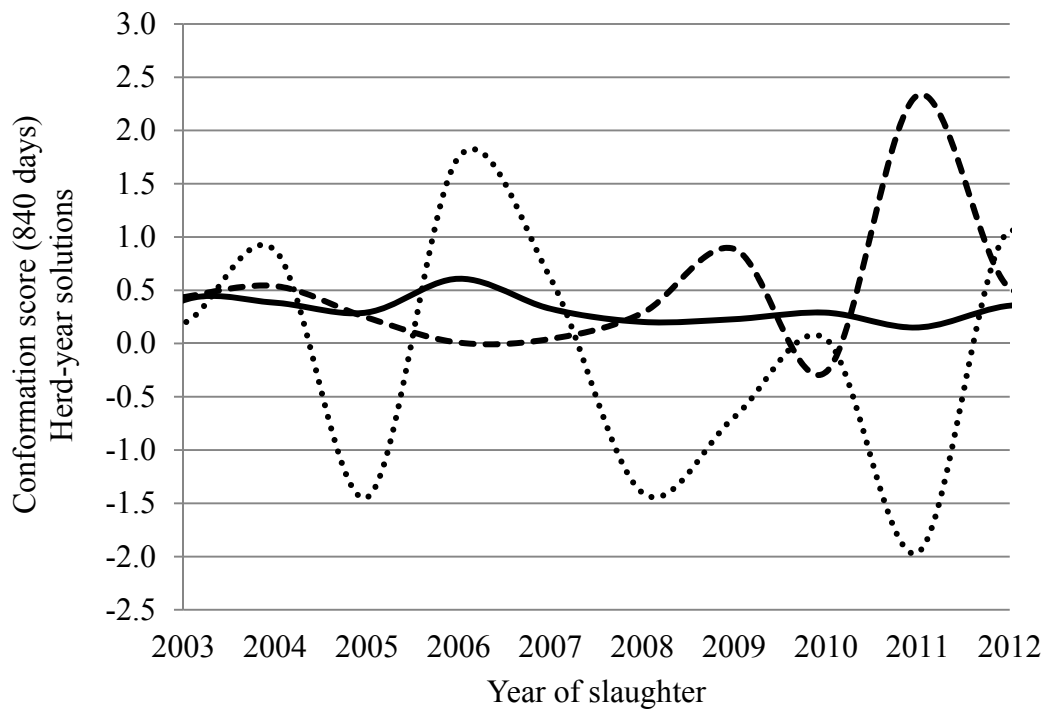
(b)



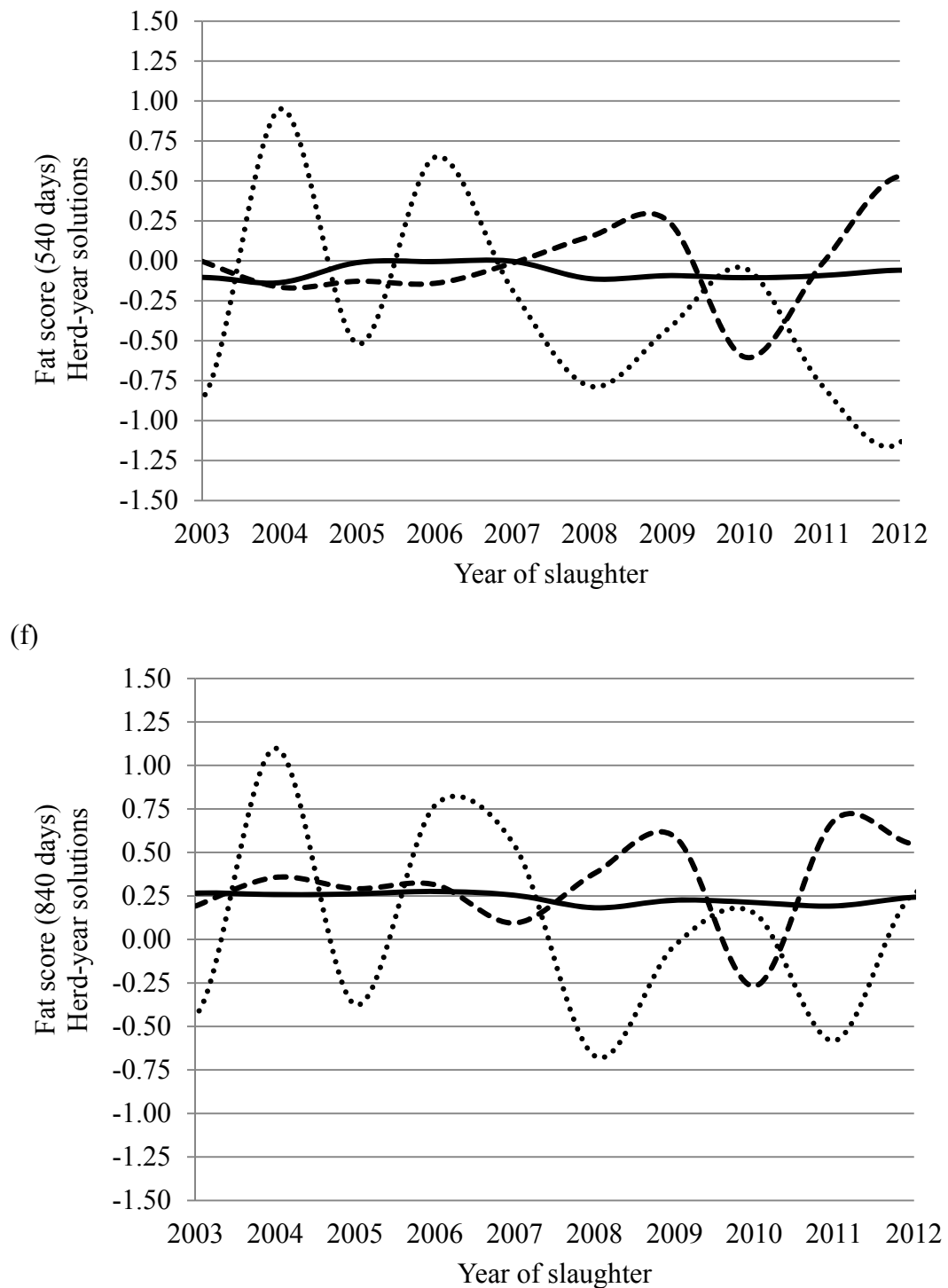
(c)



(d)



(e)



**Figure 3.6** Average (—) and individual finishing herd-year curves for carcass weight at 540 days of age at slaughter (a) and 840 days of age at slaughter (b); conformation score at 540 days of age at slaughter (c) and 840 days of age at slaughter (d); fat score at 540 days of age at slaughter (e) and 840 days of age at slaughter (f), in two finishing herds, A (· · ·) and B (— — —), of steers slaughtered between 2003 and 2012.

#### DISCUSSION



***Finishing herd-year parameters***

The contribution of genetic variability to phenotypic variation in carcass traits of cattle has been well documented elsewhere (Reverter et al., 2000; Hickey et al., 2007; Pabiou et al., 2009 and 2011a; Englishby et al., 2016). However, little attention has been given to the examination of the environmental effect estimates simultaneously generated in the genetic evaluation process. Modelling a random finishing herd-year effect across age at slaughter provides information on how environmental, mainly management, conditions may affect beef carcass trait profiles (Bormann et al., 2003). Therefore, finishing herd-year profiles, which are analogous to estimates of genetic merit for individual animals commonly used by animal breeders, can potentially be used as a management tool to monitor herd performance across years (Windig et al., 2005). Such information can also facilitate more informed management decisions through better modelling of environmental effects (Druet et al., 2003).

In conventional carcass trait genetic evaluations, the genetic effect estimates of the animals are adjusted to average management conditions. An advantage of the present study was that the model included random effects for both animal genetic merit and finishing herd-year, thereby making it possible to assess management practices independently of the genetic merit of the animals (Caccamo et al., 2010). The performance and, consequently, profitability of the herd is related to both its genetic make-up and the environment in which the animals are finished (Wilton & Goddard, 1996); therefore, breeding decisions may be suboptimal if not combined with optimum management practices and vice versa. For instance, some sires with high genetic merit for carcass traits may produce progeny that do not reach premium grades at the abattoir

due to sub-optimum management of the finishing herd, or produce premium grades but at a higher cost to the farmer than necessary.

The finishing herd environment evidently has an important influence on carcass characteristics, as, in the present study, a large proportion of total phenotypic variance in the three studied carcass traits was attributable to finishing herd-year variance. Estimates ranged from 30.83% and 71.48% for carcass weight, from 21.68% to 56.22% for conformation score and from 10.88% to 44.04% for fat score (Figure 3.1) and in some cases were higher than the corresponding trait heritability estimates (Table 3.2). Even so, the average heritability estimates for carcass weight, conformation and fat score across all ages at slaughter and gender were moderate to strong (Table 3.2), and given the large genetic variance also estimated, genetic selection on carcass traits at any age at slaughter would be feasible and further improve animal performance.

Regardless of gender, the finishing herd environment contributed more to the phenotypic variance of carcass weight than either carcass conformation score or fat score, indicating that improving carcass weight across ages at slaughter could potentially be easier to achieve than improvements in the other two traits. Nonetheless, the finishing herd-year correlations between carcass weight and conformation score were favourable (Figure 3.4) meaning that altering management conditions to increase the value of one will also lead to superior values of the other trait. On the other hand, the positive finishing herd-year correlations between carcass weight and fat score, and between conformation and fat scores were not favourable, suggesting that management practices leading to large and well-shaped carcasses will also lead to greater fat content. Nevertheless, as these correlations were less than unity, management practices may be manipulated in order to produce animals with well conformed but lean

carcasses. The most efficient use of these correlations would be their incorporation into finishing herd management indexes, similar to genetic indexes (Hazel, 1943), with appropriate weighting given to each trait depending on their respective economic values.

An example of how specific finishing herd environments may influence the performance of carcass traits is illustrated in Figure 3.5 through the graphical interpretation of finishing herd-year of slaughter solutions across age at slaughter. In general, deviations above the fixed curve for carcass weight or conformation score confirm that the management of a particular finishing herd may result in better performing animals than those on farms under average management conditions. In contrast, deviations below the fixed curve indicates that improvements in management are warranted (Figure 3.5). Furthermore, individual finishing herd deviations above the fixed curve for fat score may not be favourable as they are associated with fatter carcasses. Although some finishing herd management practices have the propensity to produce desirable carcass traits at younger ages, the same finishing herd may perform below average at older ages or vice versa. Therefore, knowledge of individual finishing herd performance for carcass traits is important so that procedures to rectify persistent unfavourable deviations can be implemented and herds can adopt practices to improve performance.

#### ***Variation in finishing herd-year effects across age at slaughter***

The within-gender variability observed among finishing herd-years for different ages at slaughter suggests that different management practices may be more applicable for differently aged cattle within finishing herds (Figure 3.1). For example, for carcass weight in heifers and steers, the finishing herd environment had a greater influence at

early ages of slaughter. Therefore, a greater opportunity potentially exists for management practices to alter carcass weight in younger than in older heifers or steers. The opposite was evident for young bulls, where for the influence of finishing herd-year on carcass weight was greatest at older ages at slaughter.

The presence of variability in finishing herd-year effects across traits and genders was further investigated through the examination of the respective (co)variance matrices. The resulting eigenvalues and eigenfunctions confirmed significant variability among finishing herds in the shape of the carcass trait profiles. The direction of the largest eigenfunctions associated with the leading eigenvalues for all traits and genders was consistent across age at slaughter, suggesting that the corresponding proportion of finishing herd-year variation was explained by environmental factors acting similarly in all ages. However, as the second and third eigenvalues combined accounted for between 6.70% (fat score in young bulls) and 51.37% (fat score in heifers) of the total phenotypic variation, this suggests that a substantial proportion of management effects may not be the same across all ages at slaughter. All second and third eigenfunctions for the three traits had steep trends and sign changes across ages at slaughter, in agreement with the weakening of finishing herd-year correlations with increasing age distance (Figure 3.3); this therefore suggests that beef carcass traits at younger and older ages at slaughter are influenced by different management factors. The less than unity correlations between herd-year effects across different ages at slaughter for all traits and genders (Figure 3.3) also imply that modifying on-farm conditions to alter carcass traits at young ages will have lesser effect on carcass traits at older slaughter ages. This highlights the potential for farmers to focus on finishing beef for a particular end point. Indeed, the negative

finishing-herd-year correlations between heifers carcass weight and fat score at very young versus very old age at slaughter suggests that management practices that alter carcass weight or fat score in heifers at youngest ages will have an antagonistic effect on these traits at older slaughter ages.

In addition to variability in finishing herd-year effects across herds, within-herd variability across years was also evident (Figure 3.6). Indeed the performance of animals from the same finishing herd, slaughtered at the same age across different years varied greatly, emphasizing the need for accurate and continuous evaluations of environmental effects in order to enhance management practices and performance across years. Such information could also allow producers to identify the ages at slaughter that are most profitable based on their current management systems, further enabling them to focus on finishing beef for a particular end point. For example, they may decide to adopt management practices that are more conducive to slaughtering at an earlier age.

#### ***Practical implications - Finishing herd-year solutions as a management tool***

Commercial cattle are generally determined as ready for slaughter by visual inspection of the degree of fatness within the appropriate range of live weight (Van Groningen et al., 2006). With the implementation of herd-specific trait profiles described in the present study, more informed decisions on the appropriate time to slaughter may be made in order to achieve maximum returns at the abattoir. For example, if the shape of the growth profile for a finishing herd is below average at younger ages at slaughter but above average at older ages at slaughter then this finishing herd in subsequent years should perhaps focus on slaughtering as many animals as possible at older ages and streamline its management practice accordingly. Thus finishing herds specializing in

specific slaughter ages may be established. As management practices tend to have greater effects on younger ages at slaughter, finishing herds aiming to improve carcass traits at these ages may see greater progress than those with objectives to slaughter at older ages. Moreover, the herd-specific growth profiles in the present study were relative to the population average. It may however also be possible to describe the herd-specific to any given profile.

The present study illustrates that the output from random regression models is a suitable continuous herd management tool for carcass traits across ages at slaughter (Figures 3.5 and 3.6). Potentially, the outputs from such analyses could be incorporated into a beef herd management web application that graphically displays individual herd management levels across ages at slaughter in addition to trends across years. There is also the potential for the incorporation of such analyses into prediction algorithms of likely future performance, which in turn could also be graphically displayed to identify the most optimal age at slaughter for a given genetic merit in a given herd. Such web applications have previously been developed for dairy herd management purposes (Koivula et al., 2007). Finishing herd management levels may be displayed in a variety of formats to assess herd performance compared to the average, for example as the performance across finishing herds within a certain year (Figure 3.5), or within finishing herd across different years (Figure 3.6). Such information reflecting on-farm management across time coupled with breeding information and the knowledge of actual on-farm activities may highlight practices or environmental issues that resulted in poor or improved performance, thereby offering useful insights to forecast future performance. For example, consistently inferior performance relative to expectations may reflect underlying compromised health status of the herd requiring remedial

action such as vaccination. Thus, management practices may be altered accordingly and/or contingency plans implemented for the following years. This may consequently result in fewer unfavourable deviations in finishing herd performance across subsequent years as farmers make more informed decisions to improve performance at an earlier point in time. Additionally, individual finishing herd-year solutions from a random regression model could be compared between finishing herds from similar geographical regions or herds whose animals are slaughtered at the same abattoir for benchmarking purposes.

Market trends and abattoir specifications fluctuate across time in terms of carcass classification (Grunert 2006; Hornibrook and Fearne 2001); consequently, finishing herd-year solutions can aid farmers in altering their breeding goals and on-farm conditions to produce animals more in line with the anticipated changes. Further investigation into the sources of finishing herd-year variation regarding specific conditions such as differences in pasture quality, feed allocation, herd health status, stocking rates or weather fluctuations, is desirable and results could be also incorporated into enhanced management tools creating more informed, comprehensive and efficient production systems.

### **Conclusions**

The present study demonstrates how the analysis of routinely collected abattoir data for the genetic evaluation of beef carcass traits can yield useful information for consideration in farm management and decision support tools. Knowledge of the variability in herd performance across ages at slaughter and years of slaughter is a useful indicator of management and facilitates the enhancement of best on-farm practices.

**Acknowledgments**

This study has been funded under the Teagasc Walsh Fellowship Scheme.

**3.3 Chapter conclusion**

This chapter demonstrates how the appropriate modelling of beef carcass data can improve carcass performance from both a genetic and management perspective. The study shows how the exploitation of readily available carcass data can inform herd management decisions across years. A holistic approach to carcass trait evaluations, where a breeder gets information on both genetic and environmental factors influencing herd performance would improve on-farm management and utilisation of genetic resources, and subsequently the profitability of the herd.



## **Chapter 4: Across-country genetic evaluations for carcass traits in cattle**

## **4.1 Chapter introduction**

The previous two chapters were concerned with the development of genetic and non-genetic tools for the enhancement of carcass traits performance at a national level. The potential for sire genetic growth profiles (chapter 2) to improve selection decisions, and for finishing-herd year of slaughter profiles (chapter 3) to improve management decisions is promising. Nonetheless, herd sizes in Ireland and the UK are relatively small; therefore the rate of genetic gain per generation is limited by the consequent small pool of selection candidates. At the same time, interest in international trade of beef cattle germplasm has intensified but it is not possible to directly compare the genetic merit of animals for carcass traits across country. This final experimental chapter aims to carry out an across-country genetic evaluation for carcass traits using commercial data from Ireland and the UK described in chapters 2 and 3. Accurate across-country genetic evaluations for carcass traits could help identify superior breeding sires at an international level. This in turn may increase the intensity of selection as breeders would be able to make more accurate comparisons of foreign and domestic breed stock. The results will address the third objective of this thesis. This chapter is presented in the format of a scientific manuscript prepared for submission to a peer reviewed scientific journal.

The student conducted all the work related to this chapter under guidance from her supervisors (manuscript co-authors).

## 4.2 Manuscript

### **Across-country genetic evaluations of carcass traits in beef cattle**

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<sup>1</sup>*This study has been supported under the Teagasc Walsh Fellowship Scheme.*

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### **ABSTRACT**

Carcass traits are economically important traits for beef producers. Estimated breeding values (EBVs) for EUROP carcass traits are routinely generated at national level in many countries including Ireland and the United Kingdom (UK). The objective of the present study was to explore the feasibility of across-country genetic evaluations for carcass traits (namely carcass weight, conformation and fat score) between Ireland and the UK using routinely collected abattoir data from the commercial populations in the two countries. There were 225 distinct bulls common to both countries i.e. with slaughtered progeny in both Ireland and the UK. These bulls were related to 80,707 Irish and 23,162 UK animals with carcass records in each population. Genetic correlations from bivariate animal models for carcass traits in the two countries were

almost unity, ranging from 0.92 ( $\pm$  0.31) for fat score to 0.96 ( $\pm$  0.17) for carcass weight, indicating that the carcass traits recorded in both countries are genetically practically equivalent. These strong genetic correlations between carcass traits in both countries enable the direct pooling of carcass data for the purpose of across-country genetic evaluations. The across-country carcass trait genetic evaluations described in this study makes EBV's between Ireland and the UK directly comparable and demonstrate how a greater rate of genetic gain in carcass traits per generation may be achieved through across-country genetic evaluations. The increased rate of genetic gain for carcass traits per generation achievable through across-country selection in contrast to within country selection was between 2% (conformation score in Irish animals) to 33.77% (conformation score in UK animals). This improved gain is due to greater potential intensity of selection and an overall increase in reliable EBVs when data and pedigree information from both countries are combined.

**Keywords:** Carcass traits, heritability, across-country evaluations, estimated breeding values

## **INTRODUCTION**

Carcass traits are economically important traits to beef producers, and many countries including Ireland and the UK undertake national genetic evaluations for carcass traits, upon which the genetic selection of breeding stock is largely based. Beef cattle breeding is now a global activity due to the international sale of seed stock across countries as breeders wish to choose from a larger pool of candidates best suited to their breeding goals (Phocas et al., 2005).

Across-country genetic evaluations can facilitate the direct comparison of bulls between countries and improve the rate of genetic gain by increasing the accuracy and

intensity of selection (Falconer and MacKay, 1996). The accuracy of genetic evaluations can partially be improved by increasing the amount of data available on relatives of individual animals. The intensity of selection can also potentially be improved by increasing the pool of candidate animals from which to choose.

So far Interbeef, the international initiative set up to develop and deploy across-country genetic evaluations in beef cattle, has been primarily concerned with genetic evaluations of purebred Limousin and Charolais cattle for weaning weight (Journaux et al., 2006; Venot et al., 2007; Pabiou et al., 2014). The majority of animals slaughtered for beef in Ireland and the UK are crossbred animals derived from commercial populations; therefore the availability of across-country genetic evaluations for multiple breeds would better serve the breeding goals in these two countries.

The objective of the present study was to collate phenotypic and pedigree data for three carcass traits namely carcass weight, carcass conformation and carcass fat from two commercial national populations (i.e., Ireland and the UK) in order to assess the feasibility of an across-country genetic evaluation for carcass traits. Comparable predictions of an animal's genetic merit between countries could facilitate more informed selection for breeders by enlarging the pool of selection candidates.

## **MATERIALS AND METHODS**

Data used for the present study were obtained from the Irish Cattle Breeding Federation (ICBF) and UK national beef carcass databases.

### ***Data***

Carcass data used in this study were the same as those used for within country analyses of carcass traits in Ireland (Englishby et al., 2016) and in the UK (Englishby et al., 2017). In summary, carcass weight (kg), carcass conformation score (scale 1 to 15; Kempster et al., 1986) and carcass fat score (scale 1 to 15; Kempster et al., 1986) records from prime slaughter animals (heifers, steers and young bulls) were available on 336,944 Irish and 147,876 UK animals (Dataset 1). These animals were progeny of 15,127 and 8,817 Irish and UK sires, respectively. Animals in the respective pedigree files of each country were identified by their international identification numbers (Pabiou et al., 2007). Genetic connections between Ireland and the UK were established through identifying sires, grandsires and great-grandsires common to both the Irish and UK populations. In total there were 225 distinct males forming 444 genetic connections established between the animals slaughtered in the Irish and UK populations. These connections were from 56 sires, 73 grandsires and 87 great-grandsires common to both populations. Each bull in each population was capable of forming multiple connections because it could match to sires, grandsires or great-grandsires in the other population, therefore, the number of connections exceeded the number of distinct bulls common to both populations. The other connections were between 112 bulls occurring as sires in one population that were recorded as grandsires or great-grandsires in the other population, and 116 grandsires that were recorded as great-grandsires in the other country. The carcass trait data in both countries were restricted to the progeny, grand-progeny or great-grand-progeny descending of these common male ancestors. Following these restrictions 35,855 Irish and 4,436 UK carcass records remained. The herd contemporaries of these progeny based on contemporary groups of finishing herd-year of slaughter were returned to their

respective data subsets. The resulting data subsets contained 109,225 Irish and 24,548 UK carcass records. For the purposes of genetic parameter estimation, data subsets were restricted to the first 50 progeny born per sire to remove bias from heavily used sires. The data subsets for genetic parameter estimation contained 80,707 and 23,162 Irish and UK carcass records respectively (Dataset 2). An across-country pedigree file was built for all animals with records in the full data set and contained five generations of most informative back-ancestry.

### ***Data analysis***

#### ***Variance component and genetic parameter estimation***

Variance component and genetic parameter estimation was based on Dataset 2 and divided into three main steps. Firstly, within country genetic parameters (heritabilities) for carcass traits were estimated using linear animal mixed models in AsReml (Gilmore et al., 2009). Secondly, genetic correlations were obtained from bivariate analyses of carcass traits in Ireland with their respective carcass traits in the UK (e.g. carcass weight in Ireland with carcass weight in the UK) using genetic parameters from the within country analyses as initial starting values. Thirdly, new genetic parameter estimates were obtained after combining data for the two countries assuming therefore a correlation of unity between carcass traits in both countries.

The mixed model fitted for the estimation of variance components in the Irish data subset was

$$Y_{dhjkmz} = \mu + a_1.Age + Sex_d + Parity_h + a_2.Het + a_3.Rec + c_m.Breed + Abattoir - DoS_j + HYS_k + Animal_z + e_{dhjklmz} \quad (1)$$

The mixed model fitted for estimation of variance components in the UK data subset was

$$Y_{dhjklmz} = \mu + a_1.Age + Sex_d + Parity_h + a_2.Het + a_3.Rec + c_m.Breed + Abattoir - DoS_j + HYS_k + BHYS_l + Animal_z + e_{dhjklmz} \quad (2)$$

Where  $Y$  = the observed records for carcass weight, carcass conformation score or carcass fatness score on animal  $z$ ;  $\mu$  = the population mean;  $a_1$  = linear regression coefficient on age at slaughter in days (Age);  $Sex$  = fixed effect of gender (heifer, steer or young bull)  $d$  of animal  $z$ ;  $Parity_h$  = fixed effect of the  $h^{th}$  parity of the dam of animal  $z$  (5 levels);  $a_2$  = linear regression coefficient on general heterosis (Het) in animal  $z$ ;  $a_3$  = linear regression coefficient on general recombination loss (Rec) in animal  $z$ ;  $c_m$  = partial regression coefficients on proportion of breed of animal  $z$ , ( $m$  summed over all 9 breeds equal unity);  $Abattoir-DoS_j$  = fixed effect of abattoir by date of slaughter interaction  $j$ ;  $HYS_k$  = fixed effect of finishing herd-year-season of slaughter  $k$ ;  $BHYS_l$  = fixed effect of Birth herd-year-season of birth  $l$ ;  $Animal_z$  = random additive genetic effect of animal  $z$ ;  $e_{dhjklmz}$  = residual error term.

In order to estimate the genetic correlation of the same carcass trait in Ireland and the UK, three bivariate analyses were undertaken using animal linear mixed models in AsReml (Gilmore et al., 2009). The bivariate model descriptions were the same as models (1) and (2). For the bivariate models, the residual covariances were fixed to zero because no animals had a carcass record in both countries.

The results from the bivariate analyses suggested that carcass traits in both countries were genetically equivalent; therefore joint variance component and genetic parameter estimation for carcass traits were carried out were the data subsets from both countries were pooled together. Joint genetic parameters for carcass weight,



conformation and fat score were generated using univariate animal models. The statistical model used in the joint analyses for each carcass trait combined the fixed effects from models (1) and (2) with an additional country fixed effect, to account for differences due to different data recording systems in each country.

#### **Calculation of estimated breeding values and reliabilities**

EBV within and across country were based on Dataset 1 (336,944 Irish and 147,876 UK carcass trait records) using the variance components derived in the previous step. Software MiX99 (Lidauer et al., 2013) was used to generate EBV and reliabilities. The statistical models of analysis were the same as for parameter estimation. Reliabilities were calculated using the approach of Tier and Meyer (2004) in ApaX (Stranden et al., 2000), which is part of the MiX99 software suite. Carcass trait EBV reliabilities from within and across-country analyses were compared and used to predict the potential response to selection (genetic gain) per carcass generation under different selection scenarios.

#### ***Predicted response to selection***

The predicted rate of gain per trait per generation ( $\Delta G$ ) was calculated separately within and across-country using the following equation (Rendel and Roberston, 1950);

$$\Delta G = i * r * \sigma_a \quad (3)$$

Where  $i$  = selection intensity;  $r$  = accuracy of estimated breeding value (selection); and  $\sigma_a$  = additive genetic standard deviation in the population.  $\Delta G$  was estimated under a number of different selection scenarios based on different truncation points (selecting top 40, top 60 or top 80 bulls within and across-country based on EBV ranking from possible selection candidates from each analysis). Selection candidates were all males

in the respective within or across-country pedigree files with carcass trait EBV reliabilities of  $\geq 0.50$ .

## **RESULTS**

Phenotypic statistics for carcass weight, conformation and fat scores for each gender in each country are in Table 4.1. On average, animals in the UK data had higher conformation and fat scores than animals in the Irish data subset, despite the former being, on average slaughtered at a younger age.

A total of 225 bulls were common to Ireland and the UK. The majority of the common sires were from dairy breeds (Holstein (50%), Friesian (20%)). Only 30% of the common sires were from beef breeds (Limousin (12%), Charolais (8%), Aberdeen Angus (5%), Hereford (2%), Blonde D'Aquitaine (2%) & Belgian Blue (1%). The proportion of Irish progeny with genetic links to the common bulls was 32%, whereas the proportion of UK progeny with genetic links to the common bulls was 17%.

Genetic correlations from bivariate models for carcass traits in the two countries were 0.96 ( $\pm 0.17$ ) for carcass weight, 0.95 ( $\pm 0.15$ ) for conformation score and 0.92 ( $\pm 0.31$ ) for fat score, indicating that the carcass traits recorded in both countries are genetically equivalent.

Estimates of variance components and heritabilities from the within and across-country models are in Table 4.2. Heritability estimates for carcass traits within and across-country were moderate to strong ranging from 0.28 ( $\pm 0.02$ ) for fat score to 0.51 ( $\pm 0.02$ ) for conformation score in Ireland, from 0.35 ( $\pm 0.03$ ) for fat score to 0.44 ( $\pm 0.03$ ) for carcass weight in the UK, and from 0.34 ( $\pm 0.01$ ) for fat score to 0.51 ( $\pm 0.01$ ) for conformation score estimated from across-country analyses (Table 4.2).

***Estimated breeding value reliabilities***

The average carcass trait EBV reliabilities of the 225 bulls common to Ireland and the UK, along with the average carcass trait EBVs for all selection candidates (bulls with carcass trait EBV reliability > 0.50) from within country analyses are in Table 4.3. There were 13,781, 5,931 and 19,712 sire selection candidates in the Irish only, UK only and across-country pedigrees, respectively. When carcass trait genetic evaluations were undertaken across-country the average EBV reliabilities for the common bulls increased compared to average EBV reliabilities when evaluations were carried out within country. The increase in mean reliabilities of EBVs for the common bulls ranged between 15.5% (conformation score in Irish compared to across-country evaluation) and 71.4% (fat score in the UK compared to across-country evaluation). For all carcass traits the UK saw a greater benefit from across-country evaluations of common bulls compared to Ireland, with increases in average reliabilities of 52.3%, 55.81% and 71.4% for conformation, carcass weight and fat score, respectively. When average EBV reliabilities for all sire selection candidates were compared, there was no improvement from across-country analyses except for conformation in the UK which saw a 1% increase in reliability estimates (Table 4.3).

**Table 4.1** Mean, standard deviation and coefficient of variation of carcass traits, by gender.

| Gender      | Trait                           | Ireland         |       | United Kingdom  |       |
|-------------|---------------------------------|-----------------|-------|-----------------|-------|
|             |                                 | Mean (s.d.)     | CV %  | Mean (s.d.)     | CV %  |
| Heifers     | Carcass weight (kg)             | 297.65 (45.27)  | 15.20 | 292.72 (35.53)  | 12.14 |
|             | Conformation score <sup>1</sup> | 7.53 (1.85)     | 24.56 | 7.32 (1.51)     | 20.63 |
|             | Fat score <sup>2</sup>          | 7.26 (1.85)     | 25.48 | 10.26 (1.55)    | 15.11 |
|             | Age at slaughter (d)            | 725.20 (134.51) | 18.55 | 676.23 (105.47) | 15.59 |
| Steers      | Carcass weight (kg)             | 346.72 (53.15)  | 15.41 | 334.06 (41.49)  | 12.42 |
|             | Conformation score <sup>1</sup> | 6.35 (2.25)     | 35.43 | 7.44 (1.48)     | 19.84 |
|             | Fat score <sup>2</sup>          | 6.67 (1.85)     | 27.73 | 9.84 (1.49)     | 15.02 |
|             | Age at slaughter (d)            | 810.26 (129.45) | 15.98 | 690.69 (108.65) | 23.82 |
| Young bulls | Carcass weight (kg)             | 368.71 (64.84)  | 17.58 | 354.27(52.18)   | 14.72 |
|             | Conformation score <sup>1</sup> | 8.80 (2.62)     | 29.77 | 9.31 (2.16)     | 24.69 |
|             | Fat score <sup>2</sup>          | 5.27 (0.99)     | 18.77 | 8.18 (2.02)     | 24.69 |
|             | Age at slaughter (d)            | 583.12 (87.61)  | 15.02 | 454.77 (53.35)  | 11.29 |

<sup>1</sup>Scored on a 15 point scale 1 (worst) to 15 (best).<sup>2</sup>Scored on a 15 point scale 1 (lean) to 15 (fat).

**Table 4.2** Phenotypic( $\sigma_p^2$ ), genetic ( $\sigma_a^2$ ) and residual( $\sigma_e^2$ ) variances, and heritability estimates ( $h^2$ )  $\pm$  (SE) for carcass weight, conformation and fat score from within country (Ireland, UK) and across country (Ireland-UK) analyses.

| Trait                           | $\sigma_p^2$  | $\sigma_a^2$   | $\sigma_e^2$   | $h^2$       |
|---------------------------------|---------------|----------------|----------------|-------------|
| Ireland (n = 80,707)            |               |                |                |             |
| Carcass weight (kg)             | 830.00 (6.19) | 380.84 (16.38) | 449.16 (12.29) | 0.46 (0.02) |
| Conformation score <sup>1</sup> | 1.18 (0.01)   | 0.60 (0.02)    | 0.58 (0.02)    | 0.51 (0.02) |
| Fat score <sup>2</sup>          | 1.13 (0.01)   | 0.32 (0.02)    | 0.81 (0.01)    | 0.28 (0.02) |
| UK (n = 20,162)                 |               |                |                |             |
| Carcass weight (kg)             | 606.36 (7.66) | 265.15 (20.25) | 341.21 (16.11) | 0.44 (0.03) |
| Conformation score <sup>1</sup> | 0.95 (0.01)   | 0.34 (0.03)    | 0.61 (0.02)    | 0.36 (0.03) |
| Fat score <sup>2</sup>          | 1.43 (0.02)   | 0.51 (0.04)    | 0.92 (0.04)    | 0.35 (0.03) |
| Ireland-UK (n = 103,869)        |               |                |                |             |
| Carcass weight (kg)             | 846.08 (5.35) | 404.17 (14.17) | 441.91 (10.75) | 0.48 (0.01) |
| Conformation score <sup>1</sup> | 1.15 (0.01)   | 0.58 (0.02)    | 0.57 (0.02)    | 0.51 (0.01) |
| Fat score <sup>2</sup>          | 1.24 (0.01)   | 0.42 (0.02)    | 0.82 (0.01)    | 0.34 (0.01) |

<sup>1</sup>Scored on a 15 point scale 1 (worst) to 15 (best).

<sup>2</sup>Scored on a 15 point scale 1 (lean) to 15 (fat).

**Table 4.3** Average reliabilities of estimated breeding value for the 225 sires common to Ireland and the UK (common sires) and for all sires from within and across country genetic evaluations with a reliability  $\geq 0.50$  (selection candidates<sup>1</sup>).

| Trait              | Average reliability<br>(common sires) | Average reliability<br>(all selection candidates) |
|--------------------|---------------------------------------|---|
| Ireland            |                                       |   |
| Carcass weight     | 0.57                                  | 0.70  |
| Conformation score | 0.58                                  | 0.71  |
| Fat score          | 0.50                                  | 0.67  |
| UK                 |                                       |   |
| Carcass weight     | 0.43                                  | 0.70  |
| Conformation score | 0.44                                  | 0.70  |
| Fat score          | 0.35                                  | 0.67  |
| Ireland-UK         |                                       |   |
| Carcass weight     | 0.67                                  | 0.70  |
| Conformation score | 0.67                                  | 0.71  |
| Fat score          | 0.60                                  | 0.67  |

<sup>1</sup>(Irish candidates n = 13,781; UK candidates n = 5,931; Ireland-UK candidates n = 19,712)

#### *Estimated response to selection*

In practice only the top ranking sires are used for breeding purposes, therefore for demonstration purposes in the present study, varying levels of selection intensities were calculated by selecting different numbers of top ranking bulls from the possible selection candidates from each analysis (Table 4.4). For all analyses within country and across-country the selection intensity decreased as the proportion of top sires selected increased. The selection intensity was greatest for all selection scenarios when sire selection was performed across-country compared to the within country sire selection (Tables 4.4).

Table 4.4 also shows the potential response to selection per generation under different selection scenarios when selection is based on each carcass trait, individually. Based on the outputs from within and across-country analyses the estimated response

to selection per generation for all carcass traits decreases as selection intensity decreases (Table 4.4). Regardless of carcass trait a greater response to selection may be achieved when selection was carried out across countries. For animals in the UK, across-country genetic evaluations could be of greater benefit for improving conformation score than carcass weight or fat score. In Ireland, fat score could benefit the most from across-country genetic evaluations, with a potential increase in response to selection for fat score of 15% if the top 40 sires are selected for breeding.

## **DISCUSSION**

The feasibility of across-country genetic evaluations in dairy cattle has been well documented with Interbull conducting genetic evaluations for an array of production and functional dairy traits across many different countries (Mark, 2005; Powell et al., 2008). Similarly, Interbeef has explored the feasibility of across-country genetic evaluations for weaning weight in beef cattle (Venot et al., 2009; Pabiou et al., 2014). Information on across-country genetic evaluations for carcass traits, however, is lacking. The genetic improvement of carcass traits is important in order to improve production efficiency. The present study directly combined carcass trait phenotypes and genetic information from Ireland and the UK and composed an across-country pedigree file by identifying the genetic links between countries. As with other across-country evaluation models (e.g. MACE) the EBV produced were directly comparable between bulls regardless of the country their records originated from.

**Table 4.4** Average carcass trait EBV accuracies ( $r$ ) for selection candidates, intensity of selection per selection scenario ( $i$ ), carcass trait genetic standard deviations ( $\sigma$ ) and expected response to selection per generation ( $\Delta G$ ) (percentage selection response achievable compared to across-country selection) for within country (Ireland, UK) and across country (Ireland-UK) populations.

| Selection <sup>1</sup><br>Scenario | Proportion<br>Selected (%) | <i>i</i> | Carcass weight (kg) |          |            |     | Conformation score <sup>2</sup> |          |            |     | Fat score <sup>3</sup> |          |            |     |
|------------------------------------|----------------------------|----------|---------------------|----------|------------|-----|---------------------------------|----------|------------|-----|------------------------|----------|------------|-----|
|                                    |                            |          | <i>r</i>            | $\sigma$ | $\Delta G$ | %   | <i>r</i>                        | $\sigma$ | $\Delta G$ | %   | <i>r</i>               | $\sigma$ | $\Delta G$ | %   |
| Ireland                            |                            |          |                     |          |            |     |                                 |          |            |     |                        |          |            |     |
| 1                                  | 0.29                       | 3.06     | 0.84                | 19.52    | 49.94      | 94  | 0.84                            | 0.77     | 2.10       | 98  | 0.82                   | 0.57     | 1.43       | 85  |
| 2                                  | 0.44                       | 2.93     | 0.84                | 19.52    | 47.81      | 93  | 0.84                            | 0.77     | 1.98       | 98  | 0.82                   | 0.57     | 1.37       | 84  |
| 3                                  | 0.58                       | 2.84     | 0.84                | 19.52    | 46.35      | 93  | 0.84                            | 0.77     | 1.90       | 97  | 0.82                   | 0.57     | 1.33       | 84  |
| 4                                  | 0.73                       | 2.77     | 0.84                | 19.52    | 45.20      | 93  | 0.84                            | 0.77     | 1.84       | 97  | 0.82                   | 0.57     | 1.29       | 84  |
| UK                                 |                            |          |                     |          |            |     |                                 |          |            |     |                        |          |            |     |
| 1                                  | 0.67                       | 2.80     | 0.84                | 16.28    | 38.11      | 72  | 0.84                            | 0.58     | 1.46       | 68  | 0.82                   | 0.71     | 1.63       | 97  |
| 2                                  | 1.01                       | 2.66     | 0.84                | 16.28    | 36.20      | 71  | 0.84                            | 0.58     | 1.36       | 67  | 0.82                   | 0.71     | 1.55       | 95  |
| 3                                  | 1.35                       | 2.56     | 0.84                | 16.28    | 34.84      | 70  | 0.84                            | 0.58     | 1.30       | 66  | 0.82                   | 0.71     | 1.49       | 95  |
| 4                                  | 1.69                       | 2.48     | 0.84                | 16.28    | 33.75      | 70  | 0.84                            | 0.58     | 1.88       | 66  | 0.82                   | 0.71     | 1.44       | 94  |
| Ireland-UK                         |                            |          |                     |          |            |     |                                 |          |            |     |                        |          |            |     |
| 1                                  | 0.20                       | 3.17     | 0.84                | 20.10    | 53.27      | 100 | 0.84                            | 0.76     | 2.15       | 100 | 0.82                   | 0.65     | 1.69       | 100 |
| 2                                  | 0.30                       | 3.05     | 0.84                | 20.10    | 51.25      | 100 | 0.84                            | 0.76     | 2.02       | 100 | 0.82                   | 0.65     | 1.63       | 100 |
| 3                                  | 0.41                       | 2.95     | 0.84                | 20.10    | 49.57      | 100 | 0.84                            | 0.76     | 1.95       | 100 | 0.82                   | 0.65     | 1.57       | 100 |
| 4                                  | 0.51                       | 2.88     | 0.84                | 20.10    | 48.39      | 100 | 0.84                            | 0.76     | 1.88       | 100 | 0.82                   | 0.65     | 1.54       | 100 |

<sup>1</sup>Scenario 1 = Top 40 sires selected from candidates based on EBV ranking

Scenario 2 = Top 60 sires selected from candidates based on EBV ranking

Scenario 3 = Top 80 sires selected from candidates based on EBV ranking

Scenario 4 = Top 100 sires selected from candidates based on EBV ranking

Selection candidates were all sires in the pedigree files with carcass trait EBV reliabilities  $\geq 0.5$  (Irish candidates = 13,781; UK candidates = 5,931; Ireland-UK candidates = 19,712)

<sup>2</sup>Scored on a 15 point scale 1 (worst) to 15 (best). <sup>3</sup>Scored on a 15 point scale 1 (lean) to 15 (fat).



***Connectedness***

To be reliable, across-country genetic evaluations require adequate connectedness between participating countries (Phocas et al., 2005). The present study sought to determine the connectedness between two commercial populations from Ireland and the UK. The level of genetic connectedness was low compared to values reported for other across-country dairy and beef genetic evaluations (Fouilloux et al., 2008), as in total only 225 distinct common bulls were identified between the Irish and UK populations. Approximately 50% of Irish and UK beef originate from dairy breed animals (Keane and Maloney, 2009; Simm, 1998); however, the majority of common bulls identified in the present study were of dairy breeds, possibly due to the greater use of artificial insemination in the dairy industry compared to the beef industry. In reality, it is likely that the true levels of connectedness between Ireland and the UK is greater than current data suggest; however, as sire recording is not compulsory for calf registration purposes in either country, the identification of common sires was severely restricted.

***Genetic parameter estimation***

The genetic correlations of carcass traits in Ireland and the same carcass trait in the UK from the bivariate analyses were strongly positive approaching unity.

The strong genetic correlations for carcass traits between both countries provide an indication of the degree of harmonisation of trait definitions between Ireland and the UK. Unlike other beef production traits such as weaning weight which is measured at varying ages between countries (Renand et al., 2003; Venot et al., 2007) the EUROP classification grid is a standard system for assessing carcass grade in European countries including Ireland and the UK (Kempster et al., 1986). This standardisation

of carcass grading and therefore trait definition has likely aided the strong genetic correlations between carcass traits in the two countries (Jakobsen et al., 2009).

Genotype by environment (GxE) interactions are of concern in across-country genetic evaluations, particularly when the analysis includes countries with different climates or production systems (Goddard, 1985). The strong genetic correlations between Ireland and the UK for carcass weight, conformation, and fat scores indicate that very little genotype by country interaction is to be considered in this across-country genetic evaluation model and that there would be no re-ranking of bulls regardless of the country where they are used (Cromie et al., 1998). The strong genetic correlations between the same carcass traits across-country were stronger than the estimated genetic correlation of 0.76 for weaning weights in Limousin between Irish and UK populations (Venot et al., 2007) and so carcass traits in beef cattle appear to be less affected by GxE interactions than weaning weight.

The model chosen by Interbeef for evaluations of weaning weight in beef cattle is a multi-variate across-country evaluation model assuming genetic correlations of less than unity among countries to account for GxE effects (Phocas et al., 2005). The nearly unity genetic correlations between carcass traits in the present study between Ireland and the UK facilitated the direct pooling of data between countries for the purpose of across-country evaluations (treating data from two countries as a single population). Other studies have reported strong genetic correlations between growth traits in beef cattle in different countries and favoured the use of joint evaluations where data is directly pooled (Meyer, 1995; De Mattos et al., 2000; Lee & Bertrand, 2002). De Mattos et al. (2000) using Hereford cattle from Canada, the US and Uruguay and Meyer (1995) using Angus cattle in Australia and New Zealand, investigated

genetic correlations and GxE interactions for adjusted weaning weights between countries. Both studies reported strong genetic correlations ( $\geq 0.64$ ) for weaning weights and therefore no significant GxE interactions across countries. Treating data from different countries as a single population with the same variance covariance matrices was therefore recommend for the purpose of across-country weaning weight evaluations in these two studies (Meyer, 1995; De Mattos et al., 2000).

Direct pooling of Irish and UK datasets for the purpose of across-country carcass trait genetic evaluations has advantages over the multi-variate models (Venot et al., 2007) currently used for the genetic evaluations of sires for weaning weights by Interbeef. The multi-variate model uses adjusted phenotypic weaning weights in each country as the dependent variables and allows for heterogeneous variances between countries (Schaeffer, 1994). In the across-country evaluations described in the present study the adjustment of phenotypes is not necessary nor is the arduous process of determining genetic covariance parameters for carcass traits between the two countries required, and therefore they are less computationally demanding.

The heritability estimates for carcass weight in Ireland ( $0.46 \pm 0.02$ ) and the UK ( $0.44 \pm 0.03$ ) from within country analyses and of  $0.48 (\pm 0.01)$  from the across-country analysis using the across-country pedigree were in close proximity to each other and are consistent with previously published heritability estimates of carcass weight within Irish and UK populations (Hickey et al., 2007; Pabiou et al., 2009) and elsewhere (Kause et al., 2003; Vesela et al., 2011). A moderate carcass weight heritability estimate of 0.40 was reported by Moore et al. (2017) who also analysed UK abattoir data from multiple breeds using animal models. In the present study conformation and fat score heritability estimates within and across-country analyses

were also comparable with estimates in other carcass trait studies (Rios-Utrera and Van Vleck, 2004; Crowley et al., 2011; Pabiou et al., 2011). Pabiou et al. (2011) analysed data from Irish abattoirs, also using animal models, reported varying heritability estimates for conformation and fat score ranging from 0.28 to 0.46 and from 0.27 and 0.40, respectively. The univariate within country heritability estimates for carcass weight, conformation and fat score in the present study, were, however, lower than those estimated on the same data sets using random regression models (Englishby et al., 2016; Englishby et al., 2017). Lower genetic variance parameters between random regression models and univariate models have been reported elsewhere (Strabel & Misztal, 1999; Rutten et al., 2005). In the present study contemporary groups were fitted as fixed effects, whereas in the random regression models fitted by Englishby et al. (2016; 2017) a random contemporary group was fitted, which may explain the differences in heritability estimates between studies (Bastin et al., 2009).

#### ***Estimated breeding value reliabilities***

The accuracy of EBV's and therefore the potential response to selection on those EBV's is indicated by their associated reliabilities (Gorjanc et al., 2015). Even though the number of bulls common to Irish and UK populations was relatively low in the present study, benefits of pooling data and pedigrees from both countries was evident in the carcass trait EBV reliability increases resulting in an increased level of confidence associated with the EBVs of these bulls.

Average EBV reliabilities for the common bulls differed between carcass traits with carcass weight and conformation having larger EBV reliabilities than fat score (Table 4.3). Venot et al. (2008) reported that increases in across-country reliabilities

reflect both the within country heritabilities and quantity of data available for the evaluations; therefore it is likely that the differences seen in the present study are due to the within country heritability differences (Table 4.2). Increased EBV reliabilities due to higher trait heritabilities have also been reported in simulated studies (Reverter, 1998) and in studies of fertility traits in dairy cattle (Sun et al., 2009).

The gain in average carcass trait EBV reliabilities for the common bulls also reflects the additional information associated with each bull from merging the carcass data and pedigree information between countries. The magnitude of improvement in EBV reliabilities varied between the common bulls, likely due to the data quantity and pedigree quality associated with individual bulls (Venot et al., 2008). As the results in Table 4.3 have shown, the reliability gains were greatest for carcass trait EBV's associated with UK bulls, reflecting the lower number of records in the within country UK analyses. The greater gain for the UK may also be due to different sire selection methods practiced between Ireland and the UK. Selection decisions to improve carcass traits in the UK have been primarily made using proxy traits of live weight and ultrasonic muscle and back-fat measurements (Moore et al., 2017). The very small gain in EBV's for the majority of selection candidates from the across-country analyses compared to the within country analyses, is likely due to their lack of connectedness between the two populations and highlights the need for improved parentage recording in both countries. Similar finding were reported by Tosh and Wilton (1994) who found no improvement in the accuracy of genetic evaluations from the addition of non-related individuals.

#### ***Predicted response to selection***

The present study demonstrates the potential benefits to beef breeders in Ireland and the UK from across-country carcass trait genetic evaluations. The strong genetic correlations between the same carcass traits in Ireland and the UK facilitate selection across-country and can increase genetic gain in comparison to selection in one country, because the same number of bulls can be selected from a larger number of selection candidates, thereby increasing selection intensity (Banos and Smith, 1991; Smith and Banos, 1991; Lohuis and Dekkers, 1998).

The rate of genetic gain per generation is also related to the accuracy of genetic evaluations; however, an overall increase in accuracy was not seen in the across-country genetic evaluations in the present study, likely due to the relatively small number of bulls common to both countries. Nonetheless, there were notable increases in carcass trait EBV reliabilities for individual bulls common to Ireland and the UK and the identification of more genetic links between both countries in the future would likely improve the overall EBV accuracies.

Genetic response to selection increases more for numerically smaller populations when across-country analyses includes populations that are larger in size (Lohuis and Dekker, 1998). Some of the greater response to selection for carcass weight and conformation score in the UK population was therefore likely due to the larger volume of carcass data from the addition of the Irish data to the genetic evaluations.

The breeding objectives for beef producers aim to improve the overall economic merit of animals which is dependent on a number of traits. Selection scenarios in Table 4.4 show the maximum response to selection achievable per generation under single trait selection. These analyses were conducted to demonstrate the potential benefit

from across country evaluations. In reality, EBV's are incorporated into selection indexes upon which selection decisions are made. Sires can be ranked based on selection index values and the lower ranking animals may be removed from the breeding populations. When selecting simultaneously for increased carcass weight, improved conformation and reduced fat score, the expected rate of genetic improvement per generation would be lower for any individual trait than single trait selection responses estimated in the present study.

The availability of animal records for across-country genetic evaluations depends upon mutual interest and cooperation. Although the present analyses indicate that the UK population may benefit more from across-country carcass trait genetic evaluations than the bigger Irish population, the latter will also see some improvement in EBV reliabilities for common bulls and in predicted response to selection for all carcass traits (Table 4.4); therefore across country cooperation and the sharing of data between the two countries would offer mutual benefits.

### ***Conclusion***

A study into the feasibility of an across-country evaluation for carcass traits has been demonstrated on data from commercial populations in Ireland and the UK. Merging together carcass data and pedigree information from both countries and performing across-country genetic evaluations leads to an increased rate of genetic response to selection for carcass traits in both Ireland and the UK.

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### **4.3 Chapter conclusion**

This chapter demonstrates the feasibility of across-country carcass trait genetic evaluations between Ireland and the UK. Access to a larger pool of selection candidates will help farmers in both countries improve selection strategies to best suit their breeding goals. The greater selection intensity will result in an increased rate of genetic gain for carcass traits in both Ireland and the UK. The results from chapter 4 also pave the way for the inclusion of carcass data from other countries into across-country genetic evaluations.



## Chapter 5: General Discussion

## **5.1 Introduction**

For over a decade, carcass data from commercial abattoirs has been used for the purpose of genetic evaluations in Ireland; such data have recently also been incorporated into the UK genetic evaluations of carcass traits. The primary outputs from these evaluations are carcass trait EBVs upon which the selection of the next generation of breeding stock is based. This thesis set out to further enhance carcass trait evaluations by investigating alternative evaluation methodologies with the aim of providing additional selection and decision support tools for Irish and UK beef farmers.

Specifically, the aim of the thesis was to generate novel tools, knowledge and information for the enhancement of national and international genetic evaluations of carcass traits in beef cattle by:

1. Modelling genetic effects on carcass traits across different ages at slaughter in order to improve genetic selection tools.
2. Modelling herd effects on carcass traits across different ages at slaughter after adjustment for genetic effects in order to facilitate on-farm management practices.
3. Exploring the benefits of across-country genetic evaluations for the three carcass traits, carcass weight, conformation and fat score.

## **5.2 New methodology for the improvement of carcass traits**

Traditionally genetic evaluations for carcass traits use linear animal models and are adjusted for age at slaughter. The resulting EBVs are the primary genetic selection tools available to beef farmers for the genetic improvement of carcass traits. The

results of genetic analyses using RRM in chapter 2 show the existence of genetic variation in carcass traits across time defined by the age at slaughter of the progeny of individual sires. The corresponding heritability estimates for carcass traits across ages at slaughter were of sufficient magnitude to indicate that carcass traits at any age at slaughter may be improved by genetic selection. The benefit to farmers of using RRM for the genetic evaluation of carcass traits is that sires receive a carcass trait evaluation for all possible ages at slaughter; therefore sires can be selected based on their individual growth curves rather than an overall figure.

Using growth curves as selection tools has interested animal breeders for generations and growth curves have been produced for many livestock species including chickens (Mignon-Grasteau, 1999), pigs (Whittemore, 1986) and sheep (Giolo et al., 2009). A number of growth curve models have also been developed for the analysis of longitudinal live weight data in beef cattle (Brody 1947; Fitzhugh et al., 1976; DeNise and Brinks, 1985). Traditional growth curves assume that all animals share the same growth pattern and that growth only increases as a function of time. This is an unrealistic assumption for carcass traits as growth from birth to slaughter is not constant (Drouillard and Kuhl, 1999). The RRM applied to carcass data in chapters 2 and 3 of this thesis incorporate covariance functions (van der Werf et al., 1998; Schaeffer, 2004) where carcass trait phenotypes are represented by a continuous function across the time trajectory (Kirkpatrick et al., 1990). Unlike traditional growth curves, no prior assumptions about the shape of the curve over time are required (Meyer and Hill, 1997). The mixed RRM produce a fixed curve to reflect the overall growth trajectory in the population and individual random curves to represent the

growth curves of each animal relative to the fixed curve (Meyer and Hill, 1997), therefore facilitating selection based on individual growth profiles.

The average age at slaughter was 706 days for Irish and 607 days for UK animals, and reflects the common 24 month finishing system. Identifying animals with the genetic potential to reach optimum carcass trait levels at younger ages may be more profitable due to reduced labour and days on feed costs. Moran et al. (2016) examined the age at slaughter and cost of finishing purebred Limousin, Holstein-Friesian and Limousin-Holstein-Friesian crossbreds in the UK. Cost of finishing was based on breed, the season the animals were born and the system they were finished in. Slaughtering beef animals at 12 months of age was found to be the most profitable (Moran et al., 2016). Genetic variances for carcass traits in chapter 2 were greatest at youngest ages of slaughter indicating the potential to select for improved carcass traits at younger ages, therefore reducing production costs at the farm level. Also the genetic correlations in chapter 2 between carcass traits across age at slaughter were sufficiently different from unity, suggesting that heavier animals may also be more muscular and leaner at different ages at slaughter. The RR growth curves, therefore, illustrate the potential to select on carcass trait trajectories and to alter growth curves to meet specific breeding objectives and, therefore, help producers meet evolving market specifications.

In general, genetics are believed to be the limiting factor in carcass trait performance except for fat composition which is considered an energy depot primarily dependent on energy intake (Bennett and Williams, 1994). Nonetheless, in chapter 3 herd-year variances reflecting different management conditions had a significant influence on all carcass traits across ages at slaughter. Regardless of gender, carcass

weight herd-year variances accounted for more phenotypic variance than the corresponding genetic variances. Herd-year variances for carcass traits across age at slaughter shown in chapter 3 reveal that both breeding and management systems should be given due consideration as a means of improving beef production to meet market specifications.

Market specifications vary across different countries and market segments, and can be volatile within the same market, meaning that the optimum time at which to slaughter animals may be subject to change. In general, leaner beef is favoured by Irish (Shan et al., 2017) and UK (Van Wezemael et al., 2010) consumers because of its perceived health benefits, and by abattoirs as leaner carcasses require less processing time post slaughter (Jones, 1989). Over-fat carcasses result in reduced meat yield, and increased processing costs as the excess fat needs to be trimmed. Abattoirs in Ireland and the UK award premium prices for carcasses that fall within optimum age ranges and carcass trait categories. In an effort to produce more uniform products, abattoir specifications now favour carcasses of a given weight per level of conformation and fatness, and place restrictions on extremely heavy carcasses (Taverner, 2016). Streamlined processing and consumer demands for a consistent product are the main motivations behind these restrictions.

In general, cattle are leaner at younger ages and fat deposition increases after the animal has matured (Bennett and Williams, 1994) therefore the specific slaughtering of cattle at younger ages may better suit the demands of European consumers who generally prefer leaner beef (Verbeke, 2010). In contrast many consumers in Eastern and South Eastern Asia prefer beef with a higher fat content (Frank et al., 2016). Growth and management curves for carcass traits may help

farmers produce beef for specific markets. Farmers could select and manage cattle for specific markets and likewise abattoirs could choose to purchase cattle from farms specialising in carcasses that meet market needs. Farmers aiming to slaughter cattle at younger ages may best suit European markets, whereas older animals with greater fat cover may best suit Asian markets.

Although European markets generally prefer leaner beef, fat content in particular intra-muscular fat (marbling) is often associated with meat quality traits such as flavour and tenderness (Mateescu et al., 2015; Sakuma et al., 2017). More work into the relationship between lean beef and flavour and the identification of breeds and management conditions that produce lean, tender and flavourful beef are needed.

Beef production is a complex business and the profitability of a herd is dependent on multiple factors. The RRM used in chapter 3, may facilitate a more holistic approach to farm management as they simultaneously evaluate the genetic and environmental aspects of carcass trait development across time. Changing the genetic make-up of the herd is one way of producing animals for a particular carcass trait endpoint but, due to the generation interval of beef cattle, it is a slow process. Changing management conditions may have more immediate implications on carcass trait performance and offer real time solutions to changing market specifications. Thus, improving the genetic make-up of animals is a complementary process to enhancing management practices. Another point of complementarity is that genetic effects are long-term whereas management improvement can be immediate.

### **5.2.1 Direct applications and further research**

Direct applications of the outcomes of this thesis pave the way for improvements in national carcass traits evaluations in Ireland and the UK based on appropriate age at

slaughter. Farmers will have the necessary tools to select sires based on their individual growth profiles. The progeny of these sires may then be managed under optimum conditions to produce carcasses in line with target market specifications.

The outcomes of this thesis leave further scope for research including the application of RRM to the analysis of other carcass traits such as individual carcass cuts. In all Irish abattoirs and increasing numbers of UK abattoirs, carcasses are graded using VIA software, which also has the capacity to predict individual primal cut yields (e.g. fillet, striploin, topside, knuckle, silverside and rump) that are of high value to the processors and consumers (Pabiou et al., 2011a; 2011b). It has been suggested that a system that rewards producers according to the quantity of high value retail cuts would be more logical than the current EUROP grading systems in place (Pabiou et al., 2009). If this payment system is implemented, tools for the genetic selection of high value cuts shall be warranted.

The influence of management on carcass trait performance in chapter 3 was modelled at the level of herd-year of slaughter. Another possible approach is to model management effects based on production system (e.g. intensive, semi-intensive, extensive). The optimum sires, management systems and therefore ages at which to slaughter animals may vary depending on production system.

Further studies may also focus on the specific factors responsible for this variation in performance due to herd management. Some of these factors may be beyond farm level control (e.g., climate), but others are likely subject to altered management practices (e.g., feeding system, stocking rate, etc.). Cattle in Ireland and the UK are predominately reared outdoors and are therefore vulnerable to extreme changes in environmental conditions. Periods in which weather patterns were

unseasonably dry or wet may be a source of variation contributing to the herd-year variations. Climate change has been estimated to have a negative effect on livestock production worldwide (Nienaber et al., 1999) and long term changes in weather patterns due to climate change may have severe implications on beef production (Nardone et al., 2010). Geographical location and climate will also influence pasture quality and quantity which in turn impact average daily gain (ADG) and subsequently carcass trait performance (Gaertner et al., 1992; Schlegel et al., 2000). The stocking rate of cattle on pasture is also of concern to carcass performance as in general ADG per animal decreases with increasing stocking rate (Derner et al., 2008). Geographical proximity to the abattoir may also influence the grades carcasses are awarded. Long transport periods from farm to abattoir can negatively affect carcass weight, yield and quality due to long periods without food or water intake (Schaefer et al., 2001), stress (Schwartzkopf-Genswein et al., 2012) and carcass bruising (Jarvis, 1995; Heurtas, et al., 2015) which result in the down grading of carcasses (Gallo et al., 2008).

### **5.3 Benefits of across-country genetic evaluations for carcass traits in cattle**

Chapter 4 concentrated on developing across-country carcass trait genetic evaluations between Ireland and the UK, and showed how such cooperation could increase genetic gain for carcass weight and EUROP graded conformation and fat scores in both countries. Increases in genetic gain were primarily due to greater selection intensity as carcass trait EBVs were directly comparable between sires regardless of the country in which their progeny were reared, thereby increasing the pool of selection candidates. Farmers in Ireland can get access to the top bulls in the UK and vice versa. The ability to accurately select the best bulls across country may greatly improve genetic progress



for carcass traits but as there is very little GxE between Ireland and the UK for the studied traits the ranking of bulls for in both countries is the same. This may lead to both countries selecting the same top sires for breeding and would necessitate appropriate management of the selected animals (e.g. mating schemes, optimum contribution strategies) to avoid a loss in genetic diversity among breeds (Brotherstone and Goddard, 2005). The different economic weighting placed on the carcass traits in both countries may, however, result in different bulls being best suited to each country and help maintain the genetic variability among populations (Brotherstone and Goddard, 2005).

The accuracy of genetic predictions are equally important as the EBVs themselves, as the greater the EBV accuracy the lower the selection risk and more predictable the offspring performance (Evans, et al., 2007). In chapter 4 the overall carcass trait accuracies within Ireland and the UK were not significantly improved by the addition of data from the other country. The lack of improvement in accuracy was likely due to relatively few bulls being common to (i.e. with progeny in) both countries. Nonetheless, there were notable increases in carcass trait EBV reliabilities for the bulls common to Ireland and the UK and the development of more genetic links between both countries in the future through intensified trade would likely further improve EBV reliabilities.

The low numbers of common sires identified between the Irish and UK populations in this thesis are possibly because sire recording is not compulsory for calf registrations in either country. Unlike in the dairy industry artificial insemination (AI) is not widely practiced in commercial beef breeding, with natural service being the reproductive method of choice (Amer, 2007). The low levels of AI usage in beef

production may be due to AI not offering a large economic advantage to semi-extensive breeding herds which make up the majority of suckler herds in Ireland and the UK (Todd, 2013). Regardless of the low numbers of common bulls identified between the Irish and UK populations, the genetic correlation between carcass traits in both countries was very strong and approaching unity; therefore, a model where data from both countries was directly pooled was plausible for the across country carcass trait analyses.

If however, more countries are to be included in the analysis and GxE interactions are detected then a multi-variate across country evaluation model may be more appropriate. The level of connectedness of any further participating countries with Ireland and the UK would need to be established and will likely vary between countries depending on breed popularity and production systems. The two continental breeds most popular in Ireland and the UK are Limousin and Charolais (Moore et al., 2016; ICBF, 2014). Previous across-country studies on weaning weights have reported strong genetic links between Irish and French, and UK and French populations of Limousin and Charolais cattle (Renand et al., 2003; Venot et al., 2007) and so exploring links through the French populations may further improve across-country carcass trait genetic evaluations. Even if genetic connectedness is low between Ireland, the UK and other countries, across-country genetic evaluations may still be undertaken using herd cluster models (Weigel and Rekaya, 2000; Zwald et al., 2003). In herd cluster models, traits are defined across country borders according to management, climate and genetic composition, and have been suggested as an appropriate method of across-country genetic evaluations when connectedness is low or if significant GxE exists.

### **5.3.1 Direct and further applications of across-country genetic evaluations**

The outcomes of chapter 4 demonstrate the feasibility of implementing across-country carcass trait genetic evaluations between Ireland and the UK, through the direct pooling of data and pedigree information between both countries. Access to across-country genetic evaluations will allow farmers to directly compare bulls from Ireland and the UK and subsequently choose the best bulls suited to their breeding programmes. This will facilitate the rate of genetic gain in carcass traits in both countries.

In addition there are a number of future research projects possible that build on the results from the across-country analysis of chapter 4. For example, RRM could be the next step in the development of across-country sire selection tools. The prospect of applying RRM to across-country genetic evaluations has been explored using populations of dairy cattle from different countries (Jamrozik et al., 2002; Barrett et al., 2005; Hammami et al., 2009). Jamrozik et al. (2002) applied a multi country RRM to first lactation test day records from Canada, Italy, New Zealand and Australia. The genetic correlations between countries were significantly less than unity indicating GxE interactions, but the proportion and direction of variation was similar for all countries, with the greatest weights on production level and persistency (Jamozik et al., 2002).

EBV's from the across-country carcass trait genetic evaluations in chapter 4 rank sires independent of country, however the optimum sire for each herd may vary depending on environmental factors such as climate or production system. Alternative RRM such as reaction norm models described by Kolmodin et al. (2002)

may be suitable for identifying the optimum sires per herd to achieve optimum carcass performance and should be explored further. In the study by Kolmodin et al. (2002) random regressions were estimated for dairy bulls by regressing phenotypic progeny values on herd environments. They found that genetic parameters for protein production and days open in first lactation vary over herd environments and that sire re-ranking was a concern, particularly for lesser performing herds and that ranking lists based on an environmental herd level would be beneficial to these herds. Such models may further improve sire selection as they facilitate the identification of sires best suited to each herd or environment within a country compared to a single ranking list which is produced from the across-country analysis described in chapter 4.

The application of across-country carcass trait genetic evaluations in chapter 4 give scope to the application of across-country genetic evaluations for other traits such as carcass cut weights which could be advantageous in facilitating the rate of genetic gain in high value cuts.

Both Ireland and the UK saw benefits in EBV accuracies for common bulls through the sharing of data between countries, but the benefit was greatest for the UK which had less national data. Across-country genetic evaluations may therefore be beneficial for the improvement of difficult to measure or expensive to measure traits that are recorded in low numbers such as feed efficiency traits or methane emissions.

The validity of across-country carcass trait genetic evaluations between Ireland and the UK pave the way for across-country carcass trait genetic evaluations including other countries. There are currently 10 countries participating in Interbeef and the genetic correlations and level of connectedness for carcass traits between these countries, Ireland and the UK should be explored.

### **5.4 Knowledge transfer to farmers**

There are clear monetary incentives for farmers to breed and manage animals for improved carcass traits. The growth curves and management curves presented in chapters 2 and 3, respectively, demonstrate additional tools to aid farmers in the genetic selection and management of breed stock for improved beef production and profitability. However, the rate of improvement will be slow unless knowledge of these selection and management tools are distributed to and implemented by farmers. The financial rewards of investing in improved beef genetics has been demonstrated in a number of studies by the Teagasc and the ICBF; however, these improvements are not always extensively acknowledged by the beef industry (Cromie, 2011). Reports on beef production on both Ireland and the UK have highlighted the need for greater dissemination of research findings and genetic improvement principles to farmers (IFA, 2015; Amer et al., 2015). Initiatives such as the BETTER Farm Beef Programme in Ireland (Beehan, 2015) and the beef efficiency scheme in Scotland will help further inform farmers to the efficiency and economic benefits of improved genetics through knowledge transfer components of the programmes.

### **5.5 Benefits from efficient beef production**

Implementation of genetic selection and on-farm management tools at a national and international level described in this thesis will lead to more efficient beef production by optimising genetics and management conditions on farm. Improved production efficiency in turn has environmental benefits such by reducing greenhouse gas (GHG) emissions.

The agricultural industry has received much attention in recent years regarding its environmental impact (Capper, 2010). Methane emissions from enteric fermentation in ruminants make up approximately 12% of greenhouse gas (GHG) emissions globally (Hegarty et al., 2007) and breeding for more efficient animals may be a way of reducing GHG emissions from agriculture (Alford et al., 2006).

Genetic and management improvements that increase production efficiency result in proportionally more product made per unit feed input, as animals that reach desired carcass weight and conformation levels at faster rates than their contemporaries are likely to have better feed conversion ratios, which in turn has environmental benefits such by reducing greenhouse gas emissions (Quinton et al., 2016).

## **5.6 Conclusions**

The results presented in this thesis demonstrate how routinely collected abattoir data from Ireland and the UK are useful for the development of advanced genetic selection and on-farm management tools. Implementation of these selection and management tools can help improve the efficiency of beef production in Ireland and the UK. Furthermore, across-country carcass trait genetic evaluations are feasible and benefit both countries. Having seen the validity of across-country carcass trait genetic evaluations between Ireland and the UK based on the connectedness and genetic correlations between both countries, expanding across-country carcass trait genetic evaluations to other countries should be explored.

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## Appendix A: Residual variance estimates

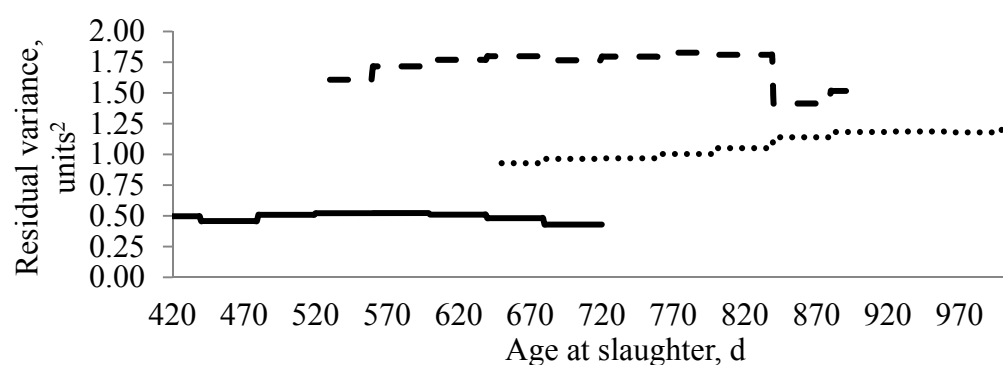
(a)



(b)



(c)



**Figure A:** Estimates of residual variance for (a) carcass weight, (b) conformation, and (c) fat in heifers (---), steers (···), and young bulls (—). Standard errors of genetic variance estimates ranged from 20.72 to 67.57 ( $\text{kg}^2$ ) for carcass weight, from 0.04 to 0.10 ( $\text{units}^2$ ) for conformation, and from 0.01 to 0.09 ( $\text{units}^2$ ) for fat. Carcass conformation and fat scores were measured on a scale of 1 to 15.